Breeding Biology and Behaviour of the Forest Raven *Corvus tasmanicus* in southern Tasmania

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ABSTRACT

The Forest Raven, *Corvus tasmanicus tasmanicus*, is the only crow or raven species found on mainland Tasmania. Although members of the genus *Corvus* have been comprehensively studied, relatively little is known about the Forest Raven. While recently studies have been made of the closely related Northern Forest Raven (*C. t. boreus*) in New South Wales, this is the first study to be undertaken on the biology of the Forest Raven in Tasmania. Overall, the results of this study suggest that Forest Ravens are similar in their breeding biology and behaviour to other corvid species with similar life-histories, both in Australia and overseas.

Adult breeding Forest Ravens maintain large self-sufficient territories year-round. Juvenile ravens remain in these territories with their parents for some months after fledging, before leaving to join nomadic flocks comprising immature birds and non-breeding adults. This study focused on the breeding biology and the behaviour of territory-holding adult Forest Ravens in six territories in light bushland around Hobart, southern Tasmania. Ravens built nests in trees characteristic of the tallest vegetation of the area, nests being situated on average 24m above the ground. The Forest Raven nesting season began in August. Incubation and nestling periods lasted around 22 days and 37-49 days respectively, with second clutches being laid in the event of the failure of the first. Forest Ravens produced on average 1.9 fledglings per pair per nesting season, with most pairs producing two fledglings. The survival rate of fledglings to one month was very high.

Away from the nest, and outside the breeding season, Forest Ravens are consistent with other bird species in spending most of their time in perching behaviour and foraging.

The Forest Raven is a common and distinctive member of Tasmania's avifauna, and is of commercial importance due to the damage it causes in orchards. Due to

the perception of the Forest Raven as an agricultural pest the species is one of only three native bird species not protected by Tasmanian law. In a number of countries corvids are becoming increasingly urban, causing problems through aggressive behaviour, noise and unsanitary mess. Although this has not yet been reported in the Forest Raven, a potential increase in food sources as a result of suburban spread in Tasmania may in the future lead to greater numbers of ravens in such areas. By providing information on the breeding and behaviour of the Forest Raven, the results of this study may be of use in the development of plans or devices to manage the species in a controlled, effective and non-lethal way.

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1. GENERAL INTRODUCTION

1.1 The breeding biology of birds

The timing and success of breeding in any given bird population is a product of many extrinsic and intrinsic factors. Breeding is an energetically expensive life history stage (Chalfoun and Martin 2007) and parents must therefore balance their own condition and survival with their reproductive output; accordingly, considerable inter- and intra-specific variation exists in all breeding parameters.

The timing of birds' breeding seasons has been the subject of investigation for many years, with relatively few changes in the underlying theories. The concept of ultimate and proximate factors influencing the timing of breeding in birds was proposed by Baker in 1938, reviewed by Lofts and Murton (1968) and is still in use today (Cockrem 1995). Breeding is one of a number of seasonal life-history stages in birds, the transitions between which are dependent on a combination of genetic and environmental factors (Wingfield 2005). Even at a small geographical scale, birds exhibit considerable inter- and intra-specific variation in the timing of breeding as a result of genetic factors and phenotypic plasticity in response to differences in environmental cues (Coppack 2007).

Ideally, young are produced at the optimum time for survival, which coincides with benign temperatures and the maximum availability of food for the maternal bird and its young (Schoech and Hahn 2007). Such long-term evolutionary strategies, or ultimate factors, determine the approximate time in which a bird population breeds each year (Cockrem 1995). Within any given year, however, the exact timing of breeding is determined by a suite of proximate cues. These proximate cues stimulate hormonal and gonadal changes in the bird, physiologically preparing the bird for reproduction, some time before actual breeding begins.

The idea that day-length determines birds' breeding seasons was introduced in the early 20th century, and has since been studied intensively (McDougal-Shackleton and Hahn 2007). Changes in photoperiod are constant year to year (Coppack 2007). In most if not all bird species, increasing day length stimulates gonadal recrudescence and associated hormonal changes preparatory for breeding (McDougal-Shackleton and Hahn 2007). At some time in the future, the bird becomes insensitive to long days, and the breeding season ends (McDougal-Shackleton and Hahn 2007). The length of birds' breeding seasons depends on the level of increase in the light phase: at higher latitudes, greater increases in the light phase in Spring result in more rapid gonadal recrudescence and a more rapid onset of photorefractoriness, and therefore a shorter breeding season than in lower latitudes (McDougal-Shackleton and Hahn 2007).

The longer and more variable breeding season of birds breeding at lower latitudes increases the reliance of such birds on non-photic environmental cues such as food availability and weather (McDougal-Shackleton and Hahn 2007; Schoech and Hahn 2007). High-latitude bird species are less responsive to increased food availability in the determination of the timing of breeding in any given year (Schoech and Hahn 2007), but are generally more reliant on photoperiod (Coppack 2007; McDougal-Shackleton and Hahn 2007).

Variation exists in the length of individual nesting stages as well as the overall timing of breeding. The time between laying and hatching is dependent on the rate of embryonic development, which in turn may be influenced by allometric constraints, predation risk or parental nest attentiveness (Martin *et al* 2007; Chalfoun and Martin 2007). Egg mass is commonly cited as a strong influencing factor on embryonic development times among bird species (Massaro *et al.* 2004), while within species the date of laying and onset of incubation, and the age of the parent birds may affect incubation periods (Massaro *et al.* 2004). As ambient nest temperature is important for efficient embryonic development (Olsen *et al.* 2006), parental nest attentiveness may influence incubation periods (Massaro *et al.* 2004; Olsen *et al.* 2006). Although birds in tropical regions exhibit lower nest

attentiveness than those in northern temperate regions (Chalfoun and Martin 2007), tropical birds do not exhibit longer incubation periods (Geffen and Yom-Tov 2000).

As with timing, the eventual outcome of a nesting event is dependent on a large number of intrinsic and extrinsic factors influencing all stages of the nesting process from the number of eggs laid and the number of those hatched, to the number of young surviving to leave the nest. Clutch sizes are variable between and within bird species. On the broadest scale, clutch sizes are generally smaller in tropical and southern hemisphere species than in northern temperate species (Martin 1996). Although a number of hypotheses have been raised in the last six decades, the reasons for this trend are unclear. These hypotheses, which include a higher rate of nest predation and lower food availability in the south and tropics than in the north, were examined by Martin (1996) who concluded that factors may interact rather than working alone. The effects of small clutch sizes on reproductive output in southern and tropical bird species may be mitigated by, or even result from, increased survival of young due to increased parental care (Martin 1996; Russell 2000).

Within species, clutches laid earlier in the season are generally larger than later clutches (Cooper *et al.* 2005). A number of hypotheses have been proposed to account for this trend. Two of these hypotheses, reviewed by Cooper *et al.* (2005), relate to temperature and may also apply to the latitudinal trend in clutch sizes. The egg-viability hypothesis suggests that, in warmer temperatures, eggs laid prior to the onset of incubation are at risk of failure; smaller clutch sizes reduce the number of eggs laid prior to incubation, which often begins after most or all of the eggs are laid (Cooper *et al.* 2005). The clutch-cooling hypothesis suggests that larger clutches are better able to retain heat in cooler temperatures (Cooper *et al.* 2005). Age also affects clutch size and reproductive output: older, more experienced birds often lay earlier and larger clutches (Robertson and Rendell 2001).

Parental care may have strong influence on the success and productivity of nesting attempts, and on the survival and fitness of young (Chalfoun and Martin 2007), however the extent of care afforded to young by their parents varies widely among bird species (Chalfoun and Martin 2007), as do the amount of care afforded by the respective male and female in monogamous pairs (Stenhouse *et al.* 2004). Direct care of young may include incubation of eggs, brooding and feeding of nestlings, and protection and feeding of fledged juveniles.

Since early in their evolution (Collias 1997), birds have constructed nests (to protect eggs and regulate the temperature of the eggs (Hansell 2000). However, the ambient temperature of the nest can be regulated further through incubation or brooding by one or both parents (Martin *et al.* 2007). In around 90 per cent of avian species, both males and females are involved in care of the young, although the amount afforded by each parent may not be equal (Stenhouse *et al.* 2004) and varies between species and breeding stages (Kokko and Jennions 2007). Birds exhibit broad geographic variation in nest attentiveness, measured as the amount of time spent incubating, which follows the geographic trends in clutch size: birds in southern and tropical areas tend to exhibit lower nest attentiveness than those in northern temperate regions (Chalfoun and Martin 2007). Food availability may influence nest attentiveness, but only within limits (Chalfoun and Martin 2007); broad geographical trends are more likely to result from latitudinal variation in adult mortality (Chalfoun and Martin 2007). While around half of the world's bird species exhibit around 90% nest attentiveness, the Passeriformes are one of only two avian orders in which nest attentiveness is generally lower than 75% (Cooper *et al.* 2005).

For many bird species the time of raising nestlings is a time of peak energy expenditure (Wright *et al.* 1998). Starvation is a major cause of nest failure (Henderson and Hart 1993), and parent birds must optimise the trade-off between adequately provisioning their current brood and maintaining their own survival and lifetime reproductive success (Wright *et al.* 1998). The rate of visits to the nest by parents during the nestling phase may be affected by a number of factors,

and may be closely related to brood size (Martin 1996). Generally, larger broods require more food; up to a limit, additional food may be provided through extra effort and increased feeding rates by parents, but may require a decrease in the selecion and nutritional value of prey items selected if the energy required of the parents becomes too great (Wright *et al.* 1998). An increase in the rate of feeding may also increase the risk of nest predation by alerting potential predators to the site of the nest (Martin 1996). A size and age hierarchy resulting from asynchronous hatching of eggs within a clutch allows for a reduction in brood size to accommodate the provisioning ability of parents if resources are limited (Krebs 1999).

Latitudinal effects on parental care extend into the post-fledging period. Russell (2000) reviewed the extent of post-fledging care in a large number of bird species and concluded that, as with clutch sizes and nest attentiveness, bird species from northern temperate regions differ from those in southern and tropical areas. The young of northern temperate species generally remain with their parents for shorter periods of time after fledging (Russell 2000). The increase in parental care both before and after fledging in southern and tropical bird species is likely to mitigate the effects of small clutch sizes, and is related to the relatively low adult mortality in these areas (Russell 2000; Chalfoun and Martin 2000).

The breeding biology of the corvids (genus *Corvus*, Corvidae) is typical of Passerine species, although variation exists even between corvid species. In his review of breeding in the British Corvidae, Holyoake (1967) reported that four *Corvus* species exhibited latitudinal variation in breeding season and two species exhibited latitudinal variation in clutch size. Four species laid larger clutches early in the season than later in the season (Holyoake 1967). While the breeding biology of corvids will form the majority of the literature cited or discussed in this thesis, in general the findings of such sources may also be applicable to other Passerine species.

1.2 The Corvids

The genus Corvus comprises the Crows, Ravens, Jackdaws and the Rook, a total of approximately 40 species world-wide (Debus 1996). Members of the genus, collectively termed the corvids, are found naturally in all regions of the world except Antarctica, South America and New Zealand, although Rooks *Corvus frugilegus* were introduced into New Zealand in the late 19th Century (Higgins *et al.* 2006). Some species, such as the Common Raven *Corvus corax*, are wide-ranging and hugely successful throughout their range, whereas others such as the Hawaiian Crow *C. hawaiiensis* and the Mariana Crow *C. kubaryi* are endangered or vulnerable and found only in small areas. Corvids have had a long association with humans; they are the subject of myth and legend from numerous cultures from all continents, from Odin's ravens Hugin (thought) and Munin (memory) of Norse mythology, to Japan and China, where crows and ravens have long been associated with the sun, to numerous Native American and Inuit legends. Crows and ravens are also found in the myths and tales of ancient and Middle Ages Europe, and in the Bible and the Talmud (Sax 2003).

1.3 The Australian Corvids

Five species of *Corvus* are found in Australia. The largest, and the only corvid found in Tasmania, is the Forest Raven *C. tasmanicus*. The Australian Raven *C. coronoides*, the Little Raven *C. mellori*, and the Little Crow *C. bennetti* are all restricted to the Australian mainland. The nominate race of the fifth Australian species, the Torresian Crow *C. orru cecilae*, is found on a number of small islands north of Australia. All five Australian corvids, along with many other species of the genus, are large, with fully black plumage. Other species have white or grey markings, but none have brightly coloured plumage (Goodwin 1977).

Worldwide, the division of corvids into "crows" and "ravens" is phylogenetically arbitrary, and is based primarily on a species' size relative to other corvids nearby; this in turn is based on the original distinction between the Common Raven

Corvus corax and the much smaller Carrion Crow *C. corone* in Britain. In Australia, this size-related distinction does not apply, as the Little Raven is significantly smaller than the Torresian Crow. The Australian corvids, despite their nominal division into crows and ravens, are more closely related to each other than to any non-Australian corvid species, except perhaps the Long-billed Crow *Corvus validus*, which is sympatric with the Torresian Crow in the Northern Moluccas (Goodwin 1977; Madge and Burn 1994); but see Vaurie (1958). In Australia, the distinction between ravens and crows is based primarily on the colour of the base of the neck feathers, with crows having distinct white feather-bases and ravens having less distinct grey feather-bases. To many Australians, however, all corvids are simply "crows".

According to the evolutionary pathway proposed by Rowley (1973d) for the five Australian corvid species, the Forest Raven separated most recently from the Little Raven, with both of these species having separated earlier from the Australian Raven *C. coronoides*. The taxonomy of the Australian corvids has been subject to many changes since the first reference to "crows" by Joseph Banks in 1770 (Rowley 1970). The Little Raven was distinguished from the Australian Raven in 1967 (Rowley 1967). The current taxonomy of the Australian corvids was completed in 1970 with the recognition of *Corvus tasmanicus* as a species incorporating two subspecies, *C. t. tasmanicus* and *C. t. boreus* (Rowley 1970). While phylogenetically the Forest Raven is most closely related to the Little Raven, for a study such as this the Australian Raven is a more useful species for comparison due to the similar size, life history and ecology of Forest and Australian Ravens.

1.4 Corvus tasmanicus

1.4.1 Identification

Like all the Australian corvids, the Forest Raven is a large-bodied bird, with a heavy bill and all-black plumage. Adults grow to approximately 55cm, with a weight of 600g – slightly larger than the very similar Australian Raven, and considerably larger than the Little Raven (Higgins *et al.* 2006). Although the Forest Raven is the largest of the Australian corvids, it is significantly smaller than the largest of the corvids, the Common Raven, in which males average around 1.2kg (Heinrich 1989). As with all corvids, sexual dimorphism in the Forest Raven is not pronounced, with the only difference being a slightly smaller body in females (Rowley 1970), although there is considerable overlap between the species and differences are almost impossible to discern in the field. In appearance, behaviour and ecology the Forest Raven is very similar to the Australian Raven; many inferences have been made about the Forest Raven's behaviour and biology based on the behaviour of the better-studied Australian Raven (Rowley 1973d; Secomb 2005). Due to the external similarities of the Australian corvids, territorial vocalizations are said to be one of the most effective features for identifying species in the wild (Debus 1995): Forest Ravens have the deepest voice of the Australian species, their territorial call being a loud, deep, harsh arr, repeated, with the last syllable often drawn out and descending in pitch.

1.4.2 Distribution

The nominate subspecies *C. t. tasmanicus* differs from the subspecies *C. t. boreus* (also known as the Relict Raven, New England Raven or Northern Forest Raven) in being slightly larger and having a shorter tail and wings (Debus 1996). The respective ranges of the two races are discrete, separated by the Kosciusko Ranges; Rowley (1973d) suggests the two races have been isolated from one another since the peak of the last glaciation, around 18000 years before present. In the past *C. t. boreus* has been recommended, but rejected, for species status (Debus 1996). The similarities found between the territorial calls of *C. t.*

tasmanicus and *C. t. boreus* (Lawrence, 2005) support the recognition of the two races as belonging to a common species.

On the Australian mainland, the Forest Raven is found in south-eastern Victoria and South Australia. In Victoria the species is restricted to three areas: the south-east coast between Gippsland and Wilson's Promontory; the Otway Ranges and surrounding areas; and around the Grampians (Figure 1.1). In South Australia the species is found only in the south-eastern corner near the Victorian border (Higgins *et al.,* 2006). The Forest Raven is thought to travel long distances across water, with individuals or flocks recorded flying between Victoria or the Tasmanian mainland and the Bass Strait islands (Sutton 1997), and between Tasmania and Maatsuyker Island (Milledge 1972). Ravens from the Tasmanian and mainland populations of *C. tasmanicus* are indistinguishable (Rowley 1973d), possibly due to genetic mixing via trans-Bass Strait travellers.

As well as mainland Tasmania, the Forest Raven is found on a number of Bass Strait Islands including Flinders (Wilmore 1977), King (Green and Mollison 1961; Peter and Starks 1993; Holdsworth 1997), Hunter (Pinner and Bird 1974; Bryant and Holdsworth 1992), Cape Barren (Whinray 1970; Harris and Harris 2002), Albatross (Brothers and Davis 1985), Clarke (Maclaine 1908; Bryant 1998), Cat (Cashion 1958) and Swan Islands(Field and Field 1989). The species is also found on Maatsuyker and surrounding islands to the south of Tasmania (Milledge 1972; Brothers 1979).

The "Relict Raven" is so named because was originally considered a small relict population of *C. tasmanicus*, found only in the New England region of New South Wales (Rowley 1970). The range of the Relict Raven, or Northern Forest Raven, has since been found to be considerably wider, with large populations on the east coast as well as an extensive area of the New England ranges (Higgins *et al.*, 2006; Figure 1.1). In Tasmania, the Forest Raven is one of the most ubiquitous bird species (Ratkowsky and Ratkowsky 1977), found in almost all habitats including wet and dry sclerophyll forests, eucalypt woodlands, beech

(*Nothofagus*) forests, alpine areas (Ratkowsky and Ratkowsky 1977; Ratkowsky and Ratkowsky 1978), coastal habitats and beaches, agricultural areas, forestry areas and plantations (Taylor *et al.* 1997; Duckworth 2000), reflecting the wide range of food sources utilized by the species. In Victoria Forest Ravens are found almost exclusively in wet forest or beech forest, the only habitat from which they are not excluded by Australian Ravens (Rowley 1970), while in South Australia Forest Ravens are often found in pine plantations (Higgins *et al.*, 2006).

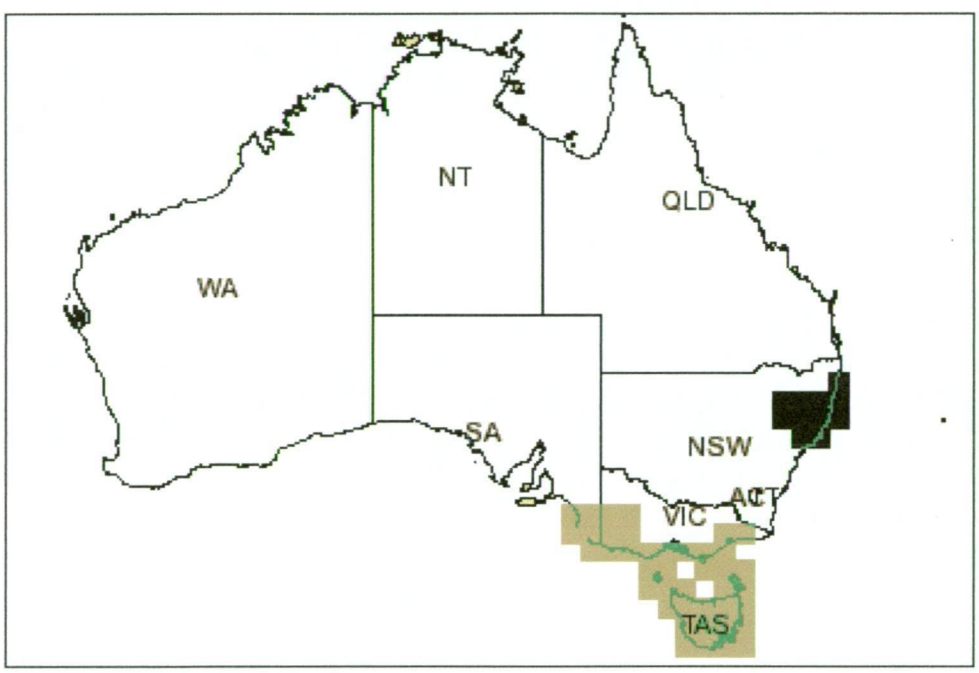


Figure 1.1 Distribution of *Corvus tasmanicus tasmanicus* (green) and *C. t. boreus* (black). Adapted from www.birdata.com.au

1.4.3 Life history

Breeding adult Forest Ravens are permanently monogamous, and defend large territories year-round. Non-territory owning adults do not breed, but form nomadic groups of "floaters", along with immature and juvenile ravens. These groups vary considerably in size: often three or four birds are seen travelling together, while hundreds of ravens can be seen feeding in areas of temporary or permanent food abundance such as freshly ploughed fields or garbage disposal

sites. Large numbers of ravens are able to overcome the defences of resident birds in whose territory they wish to feed (Rowley 1973b). While floater populations of Forest Ravens have not been studied, similar groups of Common Ravens in America have been the subject of considerable research by Bernd Heinrich, who suggests that flocking reduces aggression between individuals, promotes the formation of social alliances, and allows individuals to meet and subsequently form pairs, ready to take over a territory should one become vacant (Heinrich 1999). In Australian Ravens, a widowed territory-holding male will often obtain a new mate from a passing flock, suggesting that if pairs are formed in the flock, they are easily broken (Rowley 1973b).

Forest Raven territories may be up to 400 hectares in size (Secomb 2005). The requirements for Australian Raven territories include an appropriate tree for nesting and roosting, a water source, and various ecological niches to provide year-round food supplies (Rowley 1973b). Territories are actively defended against flocks and other pairs of ravens, including the neighbouring pairs, although territory boundaries appear to be somewhat vague (pers. obs.). As in the Australian Raven, breeding occurs in late winter and early spring. Young remain with their parents for 3-4 months after fledging (Rowley 1973d).

1.4.4 Interspecific comparisons

Many assumptions have been made about the biology and ecology of the Forest Raven, based on knowledge of the closely-related Australian Raven. Australian Ravens, Northern Forest Ravens and Forest Raven populations in Tasmania and Victoria are subject to varying environmental conditions, each of which may in some way influence the breeding biology of the population.

While the Forest Raven is the only corvid species in Tasmania, mainland populations of Forest Ravens and Northern Forest Ravens are surrounded by, or sympatric with, at least one other corvid species, leading to the potential for interspecific competition and an associated alteration or reduction in reproduction.

In New South Wales, the Northern Forest Raven is sympatric with either the Australian Raven or the Torresian Crow throughout the majority of its range (Debus 1982). Interspecific territoriality occurs (Rowley 1970; Debus 1980), although different species may occupy neighbouring territories, even occasionally share a territory (Debus 1982). A strip of forest acting as a buffer between Forest Raven and Torresian Crow may be necessary to reduce interspecific competition (Debus 1983); this was supported by Secomb (Secomb 1997), who found interspecific conflict between neighbours occurred when little or no such buffer was present. On the New South Wales coast the species is fragmented into possibly isolated populations, interspersed with cleared land inhabited by Australian Ravens and Torresian Crows (Debus 1980). Invasion of Forest Raven habitat by other species, particularly Australian Ravens, has lead to population decline and the classification of the Northern Forest Raven as "near threatened".

In Victoria the Forest Raven populations are not sympatric with, but are adjacent to populations of Australian Ravens and Little Ravens (Rowley 1970). As in New South Wales, it is likely that Forest Ravens have, in the past, been pressured by competition from Australian Ravens and consequently restricted to two discrete, isolated populations in sub-optimal breeding habitat (Rowley 1970). Mixed flocks including Forest Ravens may occur outside the breeding season (Rowley 1970). Interspecific competition may occur in such flocks when feeding, but usually the larger species dominates the smaller (Rowley 1973a); this should give the Forest Raven an advantage in such situations.

1.4.5 Previous studies

Although some information on Forest Raven breeding has been gathered through casual observation and can be found in local ornithological reports and the Birds Australia Nest Record Scheme (NRS), until now no formal study of breeding in Tasmanian Forest Ravens has been undertaken. As of December 2003, the NRS held only 19 records of Forest Raven (*Corvus tasmanicus tasmanicus*) and Northern Forest Raven (*C. t. boreus*) breeding (Higgins *et al.*, 2006). Secomb

(2005) studied a single pair of Northern Forest Ravens in New South Wales over two years; other than this, only incidental breeding observations have been recorded. Consequently, existing sample sizes for some parameters are small, and for other parameters no data have been recorded.

Rowley's study of the Australian corvids included few data for Forest Ravens, not the least reason being that the species was only recognized as separate from the Little Raven in the 1960s, during Rowley's study (Rowley 1970). A number of gaps therefore existed in the knowledge of Forest Ravens. Limited data available for Forest Ravens support a common assumption that the species is ecologically and reproductively similar to the closely-related Australian Raven (Rowley 1973c; Rowley 1973d; Rowley, Braithwaite et al. 1973; Secomb 2005), although some differences have been found. For many breeding parameters, insufficient data are available to properly determine differences between species, although the existence of more differences than are currently recognized is likely.

1.5 The Forest Raven in Tasmania

The Forest Raven is a common and familiar breeding resident in Tasmania and its offshore islands. The Birds Tasmania Garden Bird Survey of 1994-5 found *C. tasmanicus* to be the most widely dispersed of the 109 species recorded (occurring in 95% of 22 surveyed gardens); the three next most widely dispersed species were not native to the state. The Forest Raven was also the most frequently recorded species in the survey, occurring in 72% of all records, and the sixth most abundant species. The survey consequently defined Forest Ravens as "common" (Moverley 1997). In contrast, the Northern Forest Raven is classified as Near Threatened in New South Wales due to habitat loss and a related reduction in population density.

Forest Ravens, along with Australian Ravens, have long been blamed for lamb deaths in Australia, and as such have been persecuted by farmers. A study of the

effects of predation by corvids on lambs in various areas in south-eastern Australia found that crows and ravens were not a significant threat to healthy lambs in the study areas (Rowley 1969). Corvids are important in cleaning lambing paddocks of carcasses and placentas, which would otherwise provide breeding-grounds for blowflies (Rowley 1969; Jones and Park 2005). Similarly, Forest Ravens have been accused of attacking crops, but many farmers claim that crop damage by ravens is minimal, and indeed ravens may be beneficial in that they forage on crop-damaging invertebrates such as corby grubs (Jones and Park 2005). Despite the claimed benefits of Forest Ravens in an agricultural landscape the species is one of the very few native bird species not protected under Tasmanian law, being considered to cause "unacceptable damage" (Jones and Park 2005). Currently, Birds Tasmania are attempting to get the Forest Raven fully protected under Tasmanian law.

1.6 Aims

Many of the assumptions about the biology of the Forest Raven have been extrapolated from knowledge of the closely related Australian Raven, as the Forest Raven itself has not been well-studied. The current study is a preliminary investigation of breeding and behaviour of Forest Ravens in Tasmania. The data collected will be examined in the context of existing data from other corvid species, particularly the Australian Raven and the Northern Forest Raven.

Corvids are becoming increasingly urban in their life history. If this is the case in the Forest Raven, the species may require management in the future as problems arise from their presence in Tasmanian towns and cities. It has been suggested (N. Mooney, pers. comm) that a reduction in Tasmanian Devil numbers as a result of the Devil Facial Tumour Disease currently affecting the species, and the use of 1080 for eradication of browsing mammals in specific areas of Tasmania, may increase the availability of food for Forest Ravens. While the limitation of Forest Raven populations as a result of food supply has not been studied, increased food

supplies may in the future lead to increases in Forest Raven numbers in Tasmania. A knowledge of the biology of a species is vital for its management in a human landscape. This study aims to provide a basis for future studies into changes in Forest Raven populations and life history in Tasmania, while producing preliminary data which may be of use in the development of efficient, non-lethal management techniques for the species should such be required.

These aims will be addressed primarily through observation of six focal Forest Raven pairs inhabiting light bushland in southern Tasmania during the breeding seasons of 2004 to 2007 inclusive. Behavioural observations outside the breeding seasons will be made of the focal pairs as well as other ravens from around the state.

2. BREEDING BIOLOGY OF THE FOREST RAVEN IN SOUTHERN TASMANIA

2.1 Introduction

Reproduction is a vital element in the life history of any animal, and the success of this varies widely between individuals. A knowledge of the biology of breeding and factors which influence reproductive success in a given species is important in the management of that species (Soh *et al.* 2002).

Corvids exhibit a number of breeding systems. Many, including the Forest Raven, the Torresian Crow and the Forest Raven in Australia (Rowley 1973b) as well as the Common Raven (Ratcliffe 1997), are resident species which retain large breeding territories year-round. Some, such as the Australian Little Raven and Little Crow (Rowley 1973b), are territorial only during the breeding season and some, such as the Jackdaw (Henderson 1993) and the Rook (Higgins *et al.* 2006) nest colonially. Some corvid species are facultative cooperative breeders, including the American Crow (Caffrey 1992), the Northwestern Crow (Verbeek and Butler 1981) and the Carrion Crow (Richner 1990).

Between and within *Corvus* species there are variations in breeding parameters such as breeding season, clutch size, hatchability and survival. Such variation, in corvids and other birds, has been attributed to a range of environmental factors such as latitude and altitude (Lack 1947; Holyoake 1967), habitat type and characteristics (Marquiss *et al.* 1978; Richardson *et al.* 1985), predation risk, and food availability (Yom-Tov 1974). On a smaller scale, the age and experience of the parent birds may also influence reproductive success (Lack 1947; Ignatiuk and Clark 1991). Largely, however, the breeding biology and behaviour of the large resident corvid species are quite similar, even among species which have long been geographically separated.

While many studies of corvid nesting biology have been undertaken, focussing on various parameters including clutch sizes (e.g. Richardson *et al.* 1985), cooperative breeding (e.g. Baglione *et al.* 2002), nesting success (Caffrey 2000) and nestling provisioning (Henderson 1993), most of these studies have involved Northern Hemisphere corvids, particularly the Common Raven *Corvus corax*, the American Crow *C brachyrhynchos*, the North-western Crow *C. caurinus* and the colonially-nesting Jackdaw *C. monedula*. In Australia, comprehensive nesting studies have been undertaken on the Australian Raven (*Corvus coronoides*) and Little Raven (*C. mellori*), as well as the two Australian crow species (Rowley 1973c; Rowley, Braithwaite *et al.* 1973). While the Forest Raven *Corvus tasmanicus* is a highly common and ubiquitous breeding resident on the mainland of Tasmania, and has also been reported breeding on some offshore Tasmanian islands including Flinders (Barrett *et al.* 2003) and King (Donaghey 2003) Islands in Bass Strait, relatively little is known about its breeding biology. Recent studies of breeding in the Northern Forest Raven *Corvus tasmanicus boreus* by Secomb (2005) and Debus and Rose (2006) have provided some knowledge of the species, but breeding in the Tasmanian subspecies has hitherto remained virtually unstudied.

The aim of this chapter is to investigate parameters of Forest Raven breeding biology in light bushland areas of south-eastern Tasmania, including nest characteristics and use; the timing of breeding; nest productivity and survival of juveniles. The results of this study will be examined in the context of existing data from Australian Ravens and Northern Forest Ravens.

2.2 Methods

2.2.1 Study sites

Focal territories

Six Forest Raven territories in Southern Tasmania comprised the focus of this study. Two sets of neighbouring territories were included in this, from opposite ends of Kingston, south of Hobart. For clarity, each territory will be referred to in this thesis by a code-name reflecting its location, with the year in brackets when appropriate. As an example, a brood produced by the ravens in the Longley territory in 2005 would be referred to as LW01 (2005).

Approximate territory boundaries could be determined with sufficient accuracy to be confident whether a given nest was within a focal territory. A nest was deemed to be within a focal territory if the ravens from the original nest were seen to fly unchallenged around the area of the new nest; this was generally clear as ravens fly considerable distances

Nests in each territory were located through direct observation by me or others, or through the following of ravens carrying nesting material prior to breeding.

Territory 1: SL01 and Territory 2: SL02

These territories were adjoining, and were located in the Summerleas area between Kingston and Fern Tree, south of Hobart (Figure 2.1). This is a semi-rural residential area, incorporating houses and paddocks interspersed with large patches of dry sclerophyll bushland dominated by Black Peppermint (*Eucalyptus amygdalina*), Blue Gum (*E. globulus*) and *Acacia* spp. Both territories included a number of farm dams, so water was plentiful in all but particularly dry summers. Road kill was often but not always present in the area, and paddocks and trees presumably afforded large amounts of food for the resident ravens.

The SL02 territory in particular was frequented by a pair of Grey Goshawks *Accipiter novaehollandiae*, to which the resident ravens frequently showed considerable aggression. Swamp Harriers (*Circus approximans*) and occasionally Wedge-tailed Eagles (*Aquila audax*) were seen in both territories. Occasional nomadic flocks of Forest Ravens passed through the area but rarely remained for more than one or two days.

A third territory was thought to abut both of these territories, but exact boundaries could not be ascertained and active nests for the third pair were not found. Considerable territorial aggression was seen between this third pair and the SL02 pair prior to breeding.

Territory 3: PM01 and Territory 4: PM02

These territories were located in and around the Peter Murrell Conservation Area and Reserve in Kingston (Figure 2.1), an area of dry sclerophyll bush and scrubland which is popular for dog-walking and recreation. The bushland is dominated by White Gums (*Eucalyptus viminalis*), although the trees in the area are generally low compared to those in other focal territories. The PM01 territory extended across the North West Bay Golf Course, and also covered a school and suburban residential land. In addition to the reserve area, the PM02 territory contained an industrial estate and suburban residences. The nest sites within both territories were located in areas of considerable recreational usage by humans.

Brown Falcons (*Falco berigora*) and Swamp Harriers (*Circus approximans*) are known to nest in the Peter Murrell Reserve and were frequently seen flying around, although in most cases they were ignored by the ravens. Flocks of Forest Ravens are often seen in the area, particularly in summer; the nesting ravens responded aggressively to these flocks, suggesting they were seen as a threat.

While relatively little road kill would have been available to these ravens, trees and grassy areas are abundant in the area and would presumably have provided significant amounts of vegetable matter and insects. Human refuse from the

industrial and school sites nearby may have also provided food for these ravens. The conservation area incorporates a number of large permanent ponds connected by a creek; consequently water would have been readily available to the resident ravens year-round.

Territory 5: LW01

The LW01 territory was located in Longley, south-west of Hobart. The nests used by the resident ravens between 2004 and 2007 were located in a gully. The vegetation in the nest area is wet sclerophyll forest, considerably denser than the vegetation surrounding the nests of the other focal pairs in this study. Although the boundaries of the LW01 territory were not known, it is likely that the predominant vegetation type was dry sclerophyll, with some farmland and patches of wet sclerophyll forest.

The territory included a portion of the Huon Highway, which would provide a good source of road-killed carrion for ravens. It is assumed that the territory included some farm dams or other water supplies.

During observations of the LW01 nests, no intruding flock ravens were seen in the area. A Wedge-Tailed Eagle was seen once, outside the breeding season, but otherwise raptors were not seen in the nest area. The nests were located in a site which, although not far from houses, would rarely be passed by humans.

Territory 6: UT01

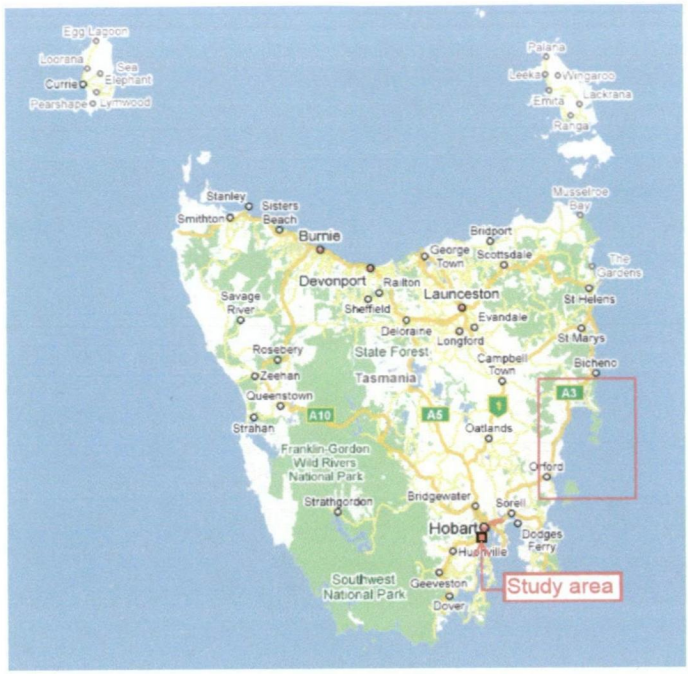
The UT01 ravens held a territory which covered much of the Sandy Bay campus of the University of Tasmania. This site consists primarily of open spaces and buildings, with an area of dry sclerophyll bushland and relatively small grassed areas. Human traffic levels were high; as a result the resident ravens were considerably less afraid of humans than the other pairs in this study.

Few raptors were seen in the nest area, and only occasional intruding ravens. Some territorial aggression occurred prior to the breeding season, between the

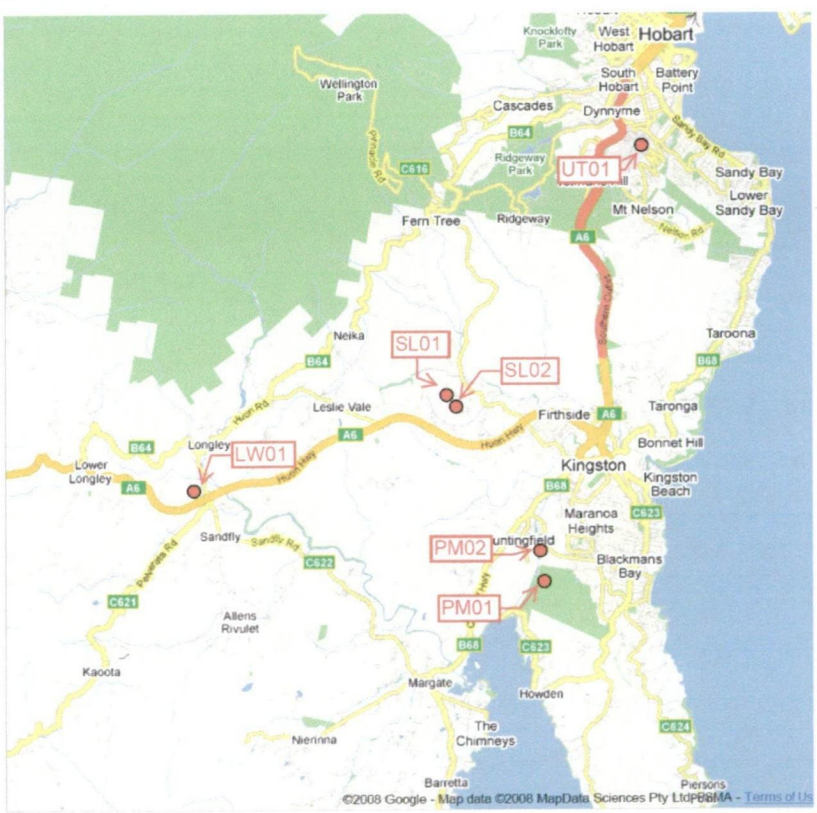
UT01 ravens and other ravens which apparently inhabited the upper portion of the campus. Depending on the boundaries of the UT01 territory, the primary food sources available to the resident ravens were most likely insects and human food scraps, with occasional carrion from surrounding roads.

Other sites

Casual observations of Forest Raven nesting, such as nest construction and productivity, were also included in this study. Such data were generally provided to me by other people and are therefore "stand alone" data points.



a



b

Figure 2.1 Sites of focal territories in southern Tasmania. *b*, detail of outlined area in *a*.

2.2.2 Nest characteristics

Study sites

As the six focal territories of this study were all located in light bushland, the characteristics of nests outside the focal territories, in different habitats, were also examined. For the purposes of this study, each nest was taken as an individual sample, regardless of the territory in which it was located. This was necessary as no data were collected on territory boundaries, potentially resulting in incorrect assumptions about nest independence.

Nest location

The height of each nest found in the focal territories was measured using a Leica LRF800 Rangefinder. If the base of the tree was accessible the measurement was taken directly, standing below the nest (Figure 2.2). Five readings were taken and an average calculated. Where the base of the nest tree was not accessible, distance to the nest was measured from a known distance from the base of the tree. This gave the horizontal and hypotenuse of a right-angled triangle, allowing calculation of the height of the nest. 1.5m was added to this (eye-height), and the result was rounded up to the nearest metre (Figure 2.2). An appropriate extra height was added to the calculated height to cover the height of the rangefinder above the base of the tree when the readings were taken (eye-height + length of rangefinder). This was usually 1.7m, but varied if the observer was not standing level with the base of the nest tree. The final figure was rounded up to the nearest whole metre, to allow for the fact that readings were taken from the base of the nest platform. The height of the nest in the tree was determined as a quartile, for instance within the top (fourth) quarter of the tree (Figure 2.3)

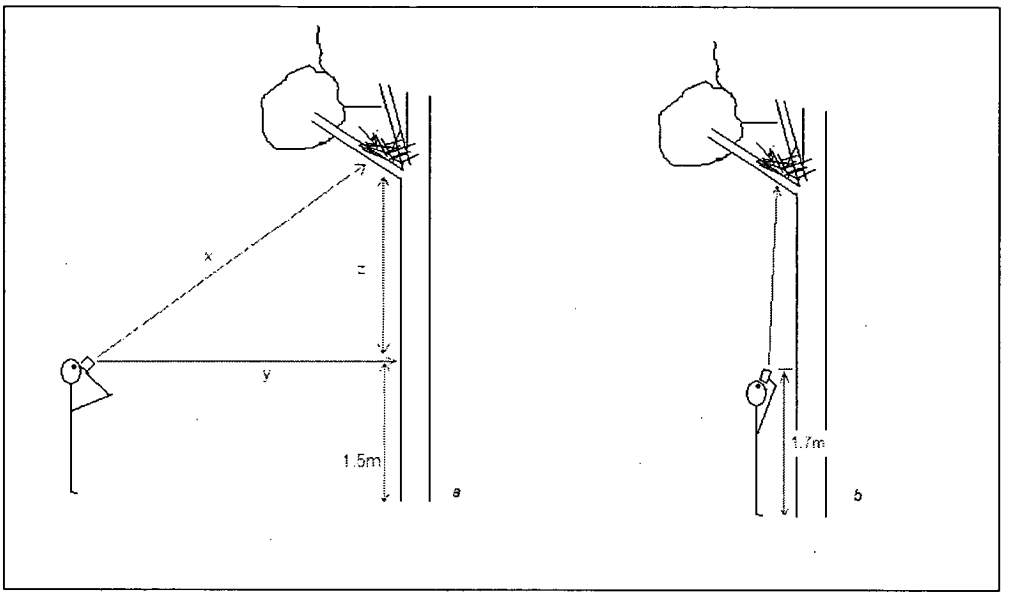


Figure 2.2 Two methods of measuring nest height using a rangefinder. a, using Pythagoras' theorem; b, direct height measurement. In each case the average of five readings is taken, and the height of the rangefinder added to the final measurement

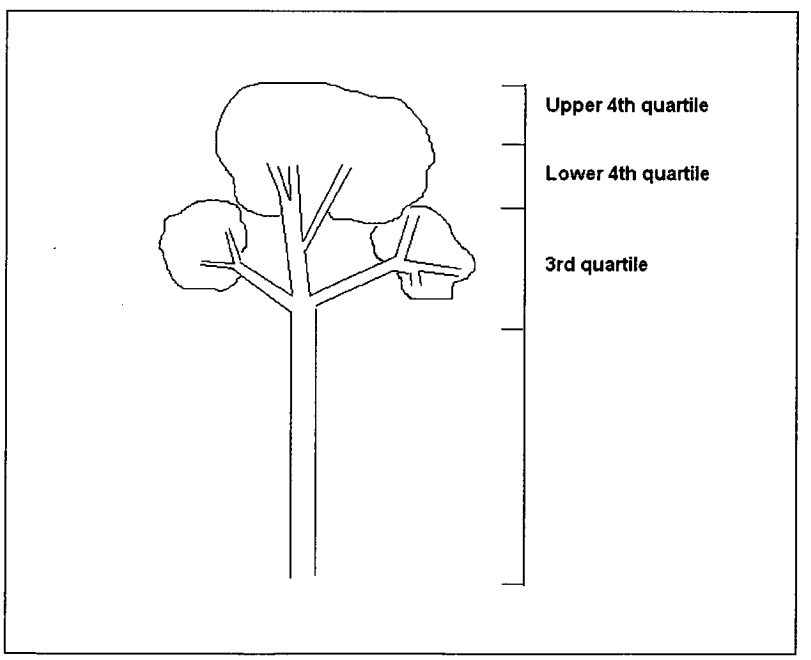


Figure 2.3 Quartiles used in descriptions of nest height relative to nest tree

As Forest Raven nests are situated in tree forks, the location of a nest in the nest tree was described according to branching order as per Rowley (1973c). Branching order is shown diagrammatically in Figure 2.4.

The characteristics of the nest tree and the location of the nest relative to other trees in the general area and specifically within a 20m radius of the nest tree were noted.

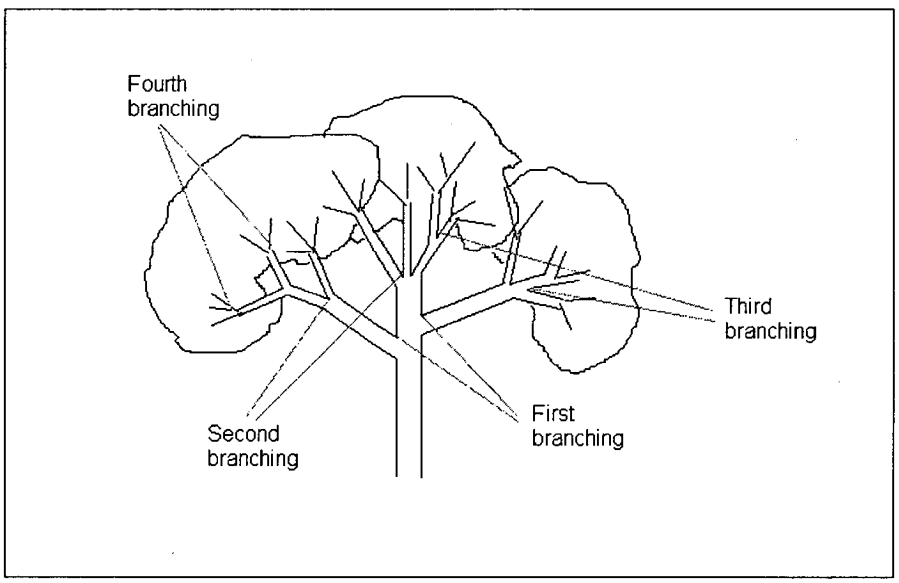


Figure 2.4 Diagrammatic representation of branching order in a typical Forest Raven nest tree. The branching order assigned to each nest is determined by the order of the fork in which that nest is situated

Nest re-use

For each observed nesting attempt the history of the nest site was recorded if known. A nest or nest site was taken to be "reused" if it had been used in the previous nesting season. Where a nest site had been used before, but not in the previous year, the ravens constructed a new nest rather than refurbishing the existing nest; in such cases the replacement nest was classified as "new".

2.2.3 Field observations

Ravens inhabiting the six focal territories in this study were observed over three (five territories) or four (one territory) breeding seasons, as well as the periods between nesting seasons. In this study the term "pair-season" will be used to describe the total reproductive activity or productivity of a given pair in a given nesting season, including both first and second nesting attempts for that season.
As this study covered only four breeding seasons for most territories, where sample sizes are inadequate for statistical comparisons with season or territory as a repeated measure, data for all territories or seasons were combined. Similarly, data were combined for averages or descriptive statistics such as overall nest productivity, in accordance with other comparable studies (e.g. Butler *et al.* 1984; Chamberlain-Auger *et al.* 1990).

Where nest construction or refurbishment was seen, the date and behaviour of the adults was noted. The ravens from three of the focal territories were studied more intensively throughout the nesting periods than those from the remaining three territories (Table 2.1). For each nesting attempt timing, success, productivity and juvenile survival were determined. The extent and type of parental care during the nesting period was determined for the four intensively-studied pairs. Each nest was visited at least twice per week from the time at which it was first located until juveniles were no longer present. Each visit lasted between 10 and 90 minutes.

Table 2.1 The six focal Forest Raven territories with the level to which they were studied over four nesting seasons. x, basic observations (nest characteristics, timing, productivity); xx, basic observations plus observations of parental care. *Data for PM01 (2006) are limited due to nest failures and are thus only included in some analyses. **LW01 nest in 2007 could not be located

Year	*Territory*					
	SL01	SL02	PM01	PM02	UT01	LW01
2004-5	x					x
2005-6	xx	x	xx	x	xx	x
2006-7	xx	x	xx*	x	xx	x
2007-8	xx	x	xx	x	xx	**

Success, productivity and survival

The success and productivity of each observed nesting attempt was determined. A nesting attempt was deemed successful if at least one fledgling was produced. A nesting attempt was deemed to have failed when the parents were not seen at the nest for more than two weeks of observations, or if they were subsequently seen to construct a new nest. Productivity was taken as the number of fledglings to leave the nest tree. Fledglings were observed for as long as possible after leaving the nest and the number of juveniles surviving to one month post-fledging was determined; by this time siblings still tended to move around together and could therefore be counted without the need to identify individuals.

Univariate Analysis of Variance was performed to test for variation in Forest Raven productivity among years, incorporating raven territory as a repeated measure.

Breeding season

For each observed nesting attempt the fledging date was estimated. For consistency, fledging date for the brood was taken as the day on which the first fledgling was seen outside the nest tree for the first time. For determination of the length of nesting stages the time between hatching and fledging was based on the day in which the first fledgling of the brood left the nest tree. The approximate length of incubation and nestling periods were determined through observations of changes in parental behaviour; these times were used to estimate laying date in cases where the onset of incubation was not observed, by counting back the appropriate number of days from the time of hatching as estimated from the onset of the provisioning of nestlings.

2.2.4 Parental care

The extent and type of parental care exhibited by Forest Ravens was determined for the the ravens inhabiting three intensively-studied focal territories in this study: SL01, PM01 and UT01. Table 2.1 shows the years in which parental care was studied in each of territories.

The time adult Forest Ravens spent incubating and brooding was determined using a two-state instantaneous sampling method. Only observation bouts lasting more than 30 minutes were used in this study. Most observation bouts lasted for one hour. The presence or absence of a raven at the nest was noted at 30-second intervals, giving a total of 120 observation points per hour. All arrivals and departures of a raven to and from the nest were noted to ensure all visits were recorded, as some visits lasted less than 30 seconds and as such may not have been detected by the instantaneous sampling. In addition, visits to incubating or brooding ravens by other ravens, and whether feeding of the incubating / brooding bird occurred, was noted. The reasons for an incubating raven leaving the nest were determined where possible.

During the brooding stages a record was made of whether a visiting bird fed nestlings. Feeding behaviour was recognised through a set of adult behaviours: a head-down position, with tail shaking, followed by raising the head and swallowing. The actions involved in feeding were initially observed in a piece of video footage of the inside of the SL01 nest during the nestling stage in 2004, and were later used as the reference for parental actions seen from the ground. As very few nest visits did not involve feeding, all visits were included in analyses.

Nest cleaning and faecal sac removal from nestlings or the nest lining was recorded; this involved the adult pecking at the inside or outside of the nest, reaching further down into the nest than during feeding, and swallowing or carrying away items from the nest. Again, these distinct actions were seen in video footage.

Each nest was observed several times throughout the breeding season, at least once per week. Observations were made at different times of day, and were classified according to diurnal period:

AM – sunrise to 1100 (AEST)
MD – 1100-1300
PM – 1300-sunset

No more than one observation bout was undertaken on an individual nest on a single day. Not all nests were observed from the beginning of the nesting period. The stage of nesting was initially estimated using parental behaviour (observed feeding of nestlings or cleaning of nest) and the approximate laying date. This was later checked against fledging date to better ensure accuracy. Each observation bout was categorised by nesting stage:

0. Incubation
1. Brooding, weeks 1-2
2. Brooding, week 3-4
3. Brooding, week 5-fledging

Each observation bout was assigned a "day after hatching", being the number of days since hatching was assumed to have occurred. These values, although not exact, were considered to be sufficiently accurate for regression analysis of the data.

Analysis

For each observation bout the proportion of time in which the nest was covered was determined as:

$$\% \text{ time on nest} = \frac{\text{number of "present" observations}}{\text{Total number of observations}} \times 100$$

During the incubation stage (Stage 0) the frequency of absences from the nest per hour was determined. For observation bouts lasting one hour a simple count was made. Given that observations were made twice per minute, giving a total of 120 observations per hour, for each observation bout lasting more or less than one hour, the mean frequency of absences per hour was determined using the equation:

$$\frac{120}{\text{number of observations}} \times (\text{number of absences})$$

If the nest was not covered at the beginning of the bout, this was counted as an absence for that hour. Mean duration of nest absences was taken as the average of absence durations for each observation bout, excluding absences in which the actual length was not known (those which began or ended outside the observation period).

During the brooding stages (1-3) the mean frequency of nest visits (visits / hour) was calculated as:

$$\frac{120}{\text{number of observations}} \times \text{(number of visits)}$$

Separate analyses of covariance (ANCOVA) were performed on the proportion of observations in which the nest was attended, and the number of visits to the nest per hour, relative to the day after hatching to test for homogeneity of slopes for each nesting season within territories. The procedure was performed using the GLM function of the SAS 9.1 software package with "Year" and "Day after hatching" as independent variables. Proportional data were arcsine transformed before analysis. Where no significant differences existed between years, the data for these years were combined for further analyses. Further ANCOVAs were performed on this combined data to identify differences among pairs, with "Territory" and "Day after hatching" as independent variables. These tests were performed on the linear regressions of the data. Non-linear regression models were developed for the proportion of time spent on the nest for each pair over time (day after hatching) using the Gauss-Newton non-linear method in the SAS 9.1 statistical software package. For all tests $\alpha = 0.05$.

Two-tailed t-tests were performed to determine differences in parental care between diurnal periods and nesting stages. Due to limited data, for these tests all nests were combined and $\alpha = 0.05$.

2.3 Results

2.3.1 Nests

Nest location

Overall the mean height of the nests measured in this study was 23.7m (n = 35), with most nests located around 19-23 metres above the ground (Figure 2.5). Mean nest height varied with habitat. Nests were significantly higher (*d.f.* = 33; $t = 3.45$; $P = 0.002$) in light bushland in southern Tasmania (25.6m; S.E. = 1.18; $n = 27$; 19-39m) than in the drier grassland areas of the Tasmanian midlands (17.1m; S.E. = 2.14; $n = 8$; 11-24m). This reflected the local vegetation: nests were generally built in the highest trees typical of the area.

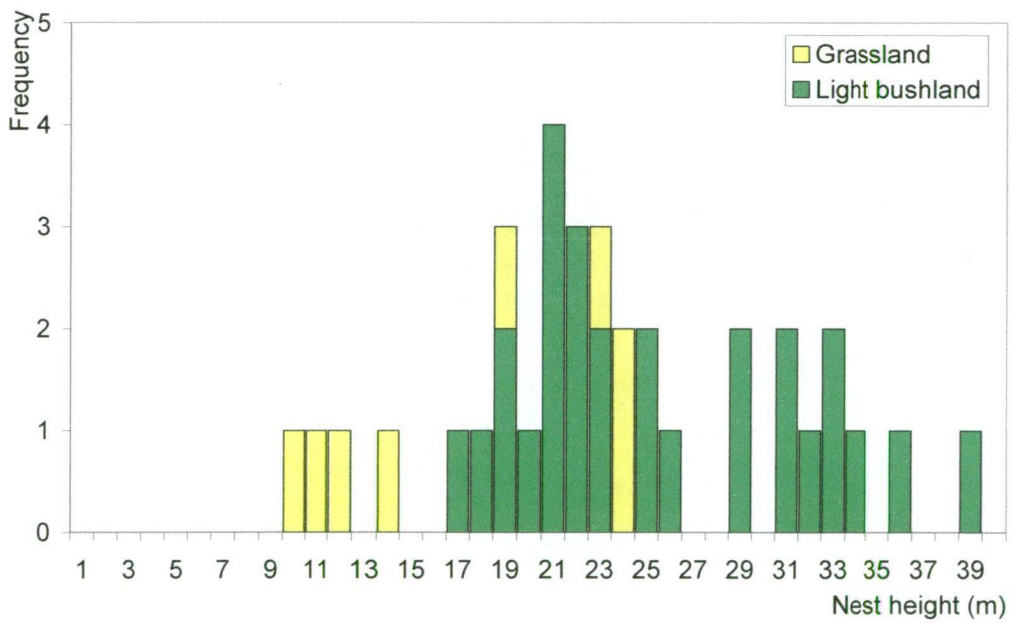


Figure 2.5 Frequency distribution of Forest Raven nest heights in Tasmania

All nests in this study provided a clear view of the surrounding area for an incubating or brooding raven, although in some cases the view in one direction may have been obstructed by the foliage of another tree. Ten out of the 35 nests studied were located in the tallest tree within at least a 20m radius. Five nests

were located in trees standing alone (no other nests within a 20m radius) with a further two being in trees with a single other tree within 20m. The remaining nests were located in trees which were typical of the highest trees in the vicinity and had open canopy foliage on at least one side of the nest.

Of the 35 nests included in the current study, 20 were situated in the top eighth of the nest tree; 14 were located in the fourth (top) quarter but not in the top eighth; and the remaining one was located in the third quarter of the nest tree (Table 2.2). Within the tree, nests were located below or on the edge of the canopy. 48.6% of the nests in this study were located in the third branching of the nest tree, with 20.0% in 4th order branchings and 17.1% in 2nd order branchings. The branching pattern of the tree largely determined the location of the nest; nests were built in as high a branching order, and therefore as far from the trunk of the tree, as the strength of the branches would appear to allow. Ravens did not appear to select nest sites based on specific branching orders; Table 2.3 shows that although suitable nest sites in different branching orders were available in each habitat, individual pairs varied in the branching order of their selected nest sites.

Table 2.2 Number of observed Forest Raven nests at different positions in nest trees for two habitat types in Tasmania.

Habitat	*Upper 4th quartile*	*Lower 4th quartile*	*3rd quartile*
Agricultural (Midlands)	2 (25.0%)	5 (62.5%)	1 (12.5%)
Light Forest (southern Tas)	18 (66.7%)	9 (33.3%)	0 (0.0%)
Total	20 (57.1%)	14 (40.0%)	1 (2.9%)

Table 2.3 Branching order of nest forks within five Forest Raven territories in southern Tasmania. Multiple values denote active nests for one or more nesting attempts for the year, and inactive nests if present. Years in brackets denote the same nest was used as in that year.

Territory	*2004*		*2005*		*2006*		*2007*	
SL01	3	3	2	2	(2005)		2	
LW01	1	1	(2004)		1			
PM01			3		1		(2005)	
PM02			4	4	3	3	3	
UT01			3		4		2	

Nest construction

Forest Raven nests comprise a deep, thick-walled bowl on a wider platform formed from large sticks propped in the fork of a tree (Figure 2.6). The inside of four nests, and the discarded lining of two others, were examined in this study. In these nests the bowl comprised medium-sized sticks tightly woven together, and incorporated both natural and man-made materials including smaller twigs, shredded bark, plus spider webs, plastic and twine. The nest bowl was lined with similar materials, grasses and feathers, bound together with mud.

Figure 2.6 Typical Forest Raven nest, showing lined bowl on larger stick platform

Both members of a raven pair are involved in nest construction or refurbishment. It was not possible to identify individual birds, but observations suggest that both males and females participate in most stages of construction. Both birds collected sticks and constructed the nest wall, although in some cases one bird collected sticks which were inserted into the nest wall by the other, which remained on the nest. This was more often the case during the lining of the nest, which was formed by one raven from materials brought by the other. Nesting behaviour was frequently accompanied by soft crooning "uh uh" noises by both birds; this was similar to noises associated with pair behaviour such as allopreening and incubation feeding (pers. obs.). The call occurred both when a raven was alone on the nest and when both ravens were present.

The construction or refurbishment of 18 Forest Raven nests was observed. Of these nests, 12 (66.7%) were being constructed or refurbished in August. Four nests were constructed or refurbished in September, including the second nest of a pair first seen building in August. Two nests were constructed in October. Some later nests were either assumed or confirmed to be new nests built after the failure of a first clutch. Some nest building may have occurred in early Autumn. The SL01 nest used in 2005 and 2006 was first seen in March 2005, but was refurbished on and around August 13 in 2005 and August 26 in 2006.

Construction of a new Forest Raven nest, or refurbishment of an old nest, was seen to last up to 13 days. In this time the ravens exhibited occasional periods of concerted building activity, lasting one hour or more, while at other times only one or two sticks were taken to the nest. In hour-long observations of nest building (UT01 2006) and nest refurbishment (PM01 2007) the ravens made 18 and 17 visits to the nest, respectively. The mean time spent on the nest per visit was 2.6 (1-6) minutes and 2.4 (0.5-7) minutes respectively. In both observations the ravens exhibited two bursts of activity, in which the nest was visited every one to two minutes, with a period of around ten minutes duration in the middle, in which time the nest was not visited. The PM01 (2007) pair were first seen refurbishing their nest on August 26, by which time considerable work had been

done. The nest was still being lined 11 days later (September 6), at which time they visited the nest six times in 30 minutes, spending between 30 seconds and two minutes on the nest at each visit.

Laying occurred between one and five weeks after observed construction or refurbishment of first nests. Second clutches were laid as soon as one day after completion of the nest.

Nest re-use

Of 15 nests of known history, two (13.3%) were used for a second consecutive nesting season. A third nest was re-built and re-used after an absence of one nesting season (two nesting attempts). This may have been the case for other "new" nests, but this was the only case in which the remains of the old nest were still at the site when a new nest was built.

Four first-clutch failures were observed in this study, all occurring during the egg stage. Second clutches were laid in the same nest in two cases; the two other failures resulted from installation of cameras at the nest, and second clutches were subsequently laid in newly constructed nests.

Extra nests

In seven of the 19 pair-seasons covered in this study a second nest was constructed close to, and at the same time as, the first nest of the pair-season. Where a second clutch was laid, and this extra nest had been built (n = 2) the second clutch was laid in a third nest, built shortly before the second clutch was laid. While these nests were not seen to be used during the day, significant quantities of excrement underneath after juveniles fledged suggested that these nests were used at night, possibly by juveniles, but this could not be confirmed.

2.3.2 Nest success and productivity

Of nineteen pair-seasons recorded in this study, 16 (84%) produced at least one fledgling. Table 2.4 gives the productivity of each observed nesting attempt. Forest Ravens in this study produced an average of 1.89 fledglings per pair-season when both first and second clutches are taken into account (S.E. = 0.24; n = 19; 0-3).

Table 2.4 Productivity of six Forest Raven territories over four nesting seasons, including first and second clutches where appropriate. Second clutches were only laid if the first clutch failed. Blank cells denote missing data. Values marked with an asterisk (*) are presumed to have been second clutches due to their late starting dates. Mean values are calculated from the total productivity of each pair in each nesting season.

	2004		*2005*		*2006*		*2007*		*Mean (territory)*
Territory	Clutch 1	Clutch 2	Clutch 1	Clutch 2	Clutch 1	Clutch 2	Clutch 1	Clutch 2	
LW01	2		2		2				2.00
SL01	2		3		3		3		2.75
SL02			1		0	0	0	0	0.25
PM01				1*	0	0	3		1.33
PM02			3		0	2	2		2.33
UT01			2			2*	3		2.33
Mean (year)	2.0		2.0		1.5		2.2		

In some cases a clutch could not be definitely identified as the first or second for the year; consequently accurate comparisons of the productivity of first and second nesting attempts could not be made. Annual productivity for pairs ranged from zero to three fledglings (Figure 2.7), with two being the most common

number of fledglings (eight of 19 pair-seasons) when all territories and seasons were considered together, although this varied among territories (Table 2.4). In all but one case (PM02 2005) all late-stage nestlings fledged successfully.

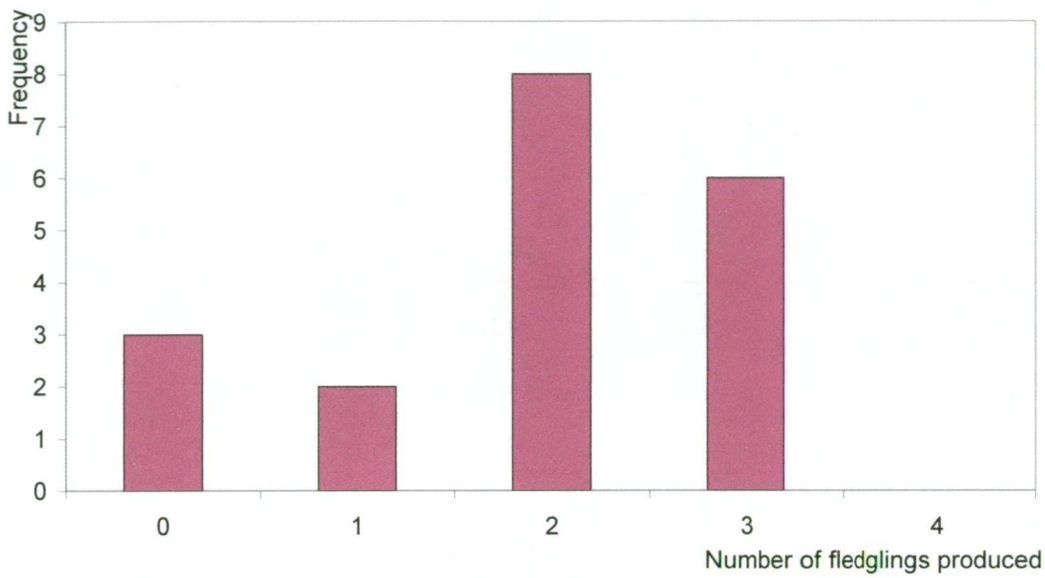


Figure 2.7 Frequency of breeding productivity in six Forest Raven pairs over four nesting seasons. n (total) = 19 pair-seasons.

In two nesting attempts, the nesting ravens failed to return to the eggs after cameras were installed at the nest In both cases, the ravens laid a second clutch, one of which failed (SL02 2006) while the other produced two successful fledglings (PM02 2006). The causes of the remaining nest failures during this study are unknown. High levels of flock activity in the vicinity of the nest at the time may have contributed to the failure of the first PM01 clutch in 2005 and the second clutch for the pair in 2006, as well as the second SL01 clutch in 2006. Of the five failures in which the timing was known, four failed at the egg stage and one failed in the first two weeks of the brooding phase. Second clutches were laid in all five known cases of failure of the first clutch. The extended period of time between the observed onset of incubation and the first observations of feeding at the SL02 nest in 2007 suggested that the first clutch failed and a second (also failed) was subsequently laid in the same nest, but this could not be confirmed.

Variation in productivity

Ravens from the SL02 territory exhibited consistently low nest productivity across the three years in which they were observed. The mean productivity of each focal territory is shown in Figure 2.8. Insufficient data were available to test these differences statistically.

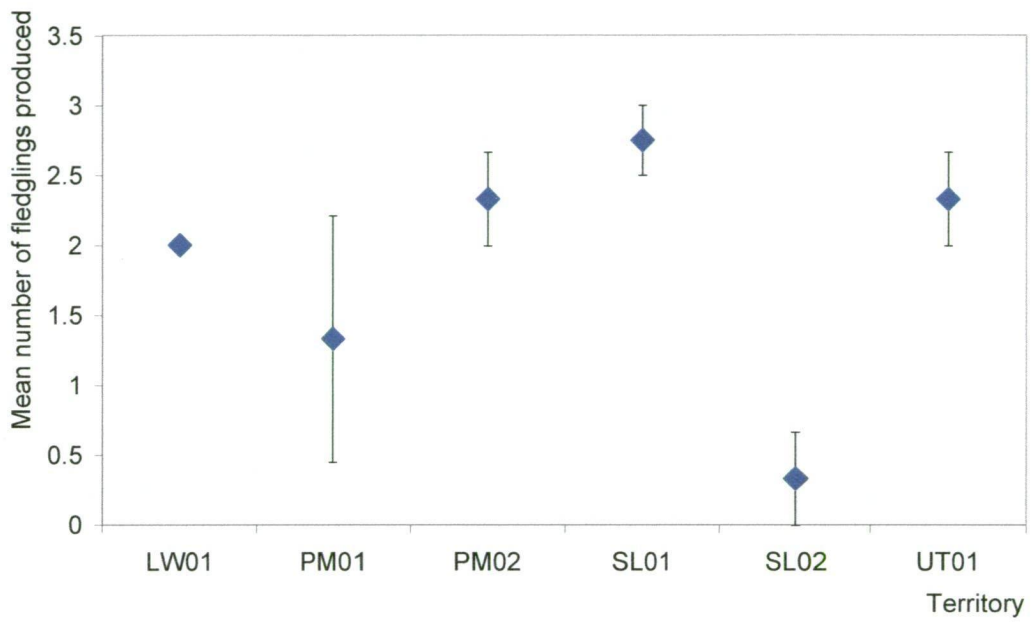


Figure 2.8 Mean productivity (± SE) of six Forest Raven territories between 2004-6 (LW01), 2004-7 (SL01), and 2005-7 (remaining pairs)

Figure 2.9 shows the mean productivity for each of the four nesting seasons of the study. Mean nest productivity was consistent within a small range (1.50- 2.25 fledglings/territory) across the four nesting seasons.

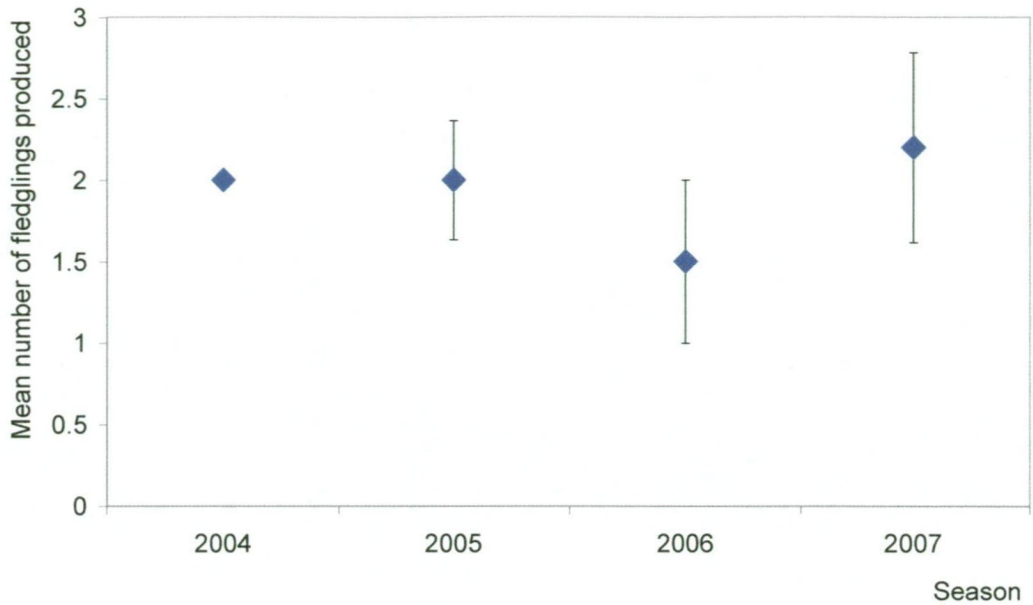


Figure 2.9 Mean productivity (± SE) of Forest Ravens over four nesting seasons. 2004, n = 2 pairs; 2005, n = 5 pairs; 2006, n = 6 pairs; 2007, n = 5 pairs. Data represent pair-seasons, or total number of fledglings produced per year per pair. Productivity did not vary significantly with nesting season ($F_{3,12} = 2.27$; $P = 0.134$)

Juvenile survival

Of 36 Forest Raven juveniles to leave the nest during this study, 35 (97.2%) survived their first month post-fledging (Table 2.5). The one juvenile not surviving its first month died within days of leaving the nest, after apparently failing its first flight and subsequently being unable to leave the ground. The cause of death in this juvenile was not determined, but no evidence of predation was found on the body.

Table 2.5 Survival of juvenile Forest Ravens to one month post-fledging in six Forest Raven territories over four pair-seasons.

Territory	*2004*		*2005*		*2006*		*2007*	
	Number fledged	*Number one month later*	*Number fledged*	*Number one month later*	*Number fledged*	*Number one month later*	*Number fledged*	*Number one month later*
SL01	2	2	3	3	3	3	3	3
SL02			1	1	0	-	0	-
LW01	2	2	2	2	2	2	2	2
PM01			1	1	0	-	3	3
PM02			3	2	2	2	2	2
UT01			2	2	2	2	3	3

2.3.3 Breeding season

The nesting season of Forest Ravens in the study area extended from late winter to mid-summer, with laying occurring between mid-August and mid-November and fledging between the beginning of November and early January (Figure 2.10). Of five nesting attempts which began on or after September 30, three were known to be second clutches for the year. The latest observed start of incubation occurred on November 9; although a previous nesting attempt was not observed for this pair in that nesting season, the timing of observed nest construction suggested that this was a second clutch.

Overall, the timing of nesting in the focal Forest Raven territories was consistent among the four nesting seasons covered by this study (Figure 2.10). The wider spread of starting dates seen in 2006 was due to relatively high frequency of nest failure in that year. The latest starting date seen in 2005, (October 8, PM01) was assumed to be a second clutch. Figure 2.11 shows that ravens in individual territories were consistent in the timing of nesting: in two territories, namely the

SL01 and LW01 territories, fledging dates ranged over five days (n=4 nesting attempts) and seven days (n=3 nesting attempts) respectively. The ravens from these territories produced successful broods in their first attempt of each of the years in which they were observed. The PM01 ravens began incubating first clutches on consecutive dates in 2006 and 2007; the other nesting attempts seen in this territory were known (2006) or assumed (2005) to be second broods. The UT01 ravens exhibited a wide spread of fledging dates, again possibly as a result of failed first clutches in 2005 and 2006. Second clutches were laid soon after a first clutch failed.

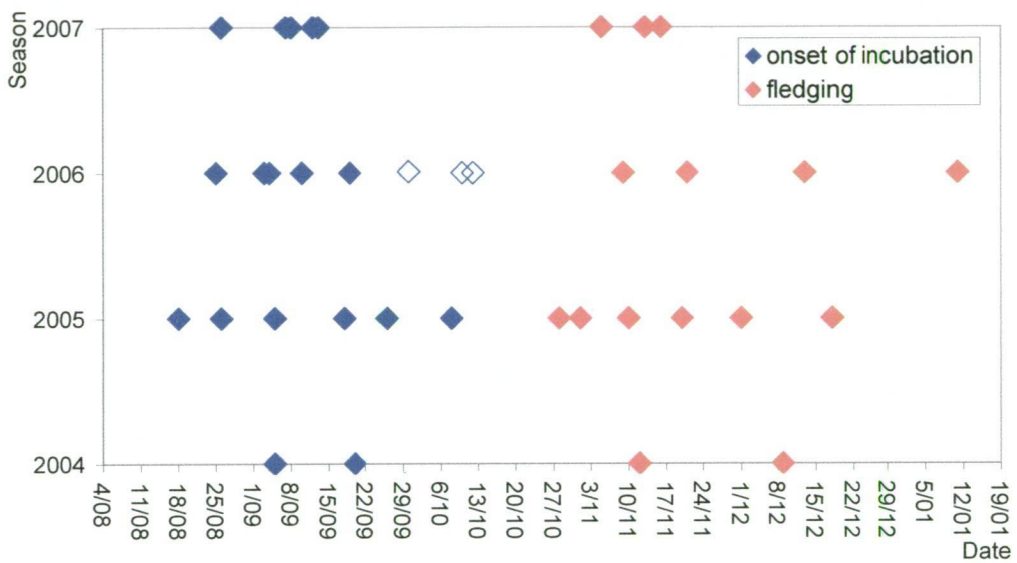


Figure 2.10 Timing of nesting in six Forest Raven territories over four breeding seasons. Open triangles signify known second clutches

Of the six focal raven territories in this study, ravens from the PM02 territory consistently laid first clutches relatively early in the season, while the LW01 ravens were the latest to lay first clutches (Figure 2.11)..

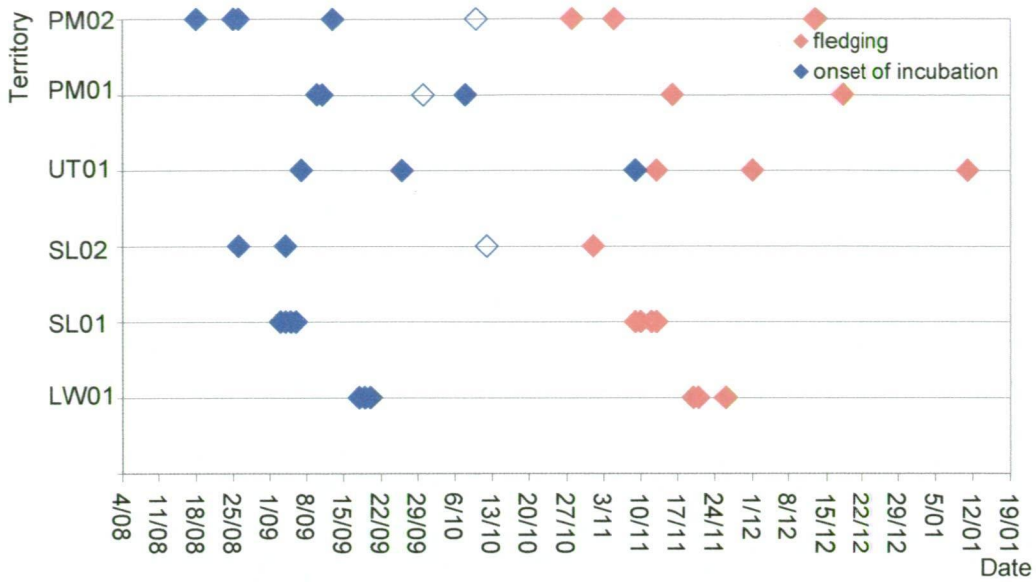


Figure 2.11 Timing of nesting in six Forest Raven pairs over four (SL01) or three nesting seasons. Open diamonds signify known second clutches

Length of nesting phases

Changes in parental behaviour consistently indicated that incubation lasted approximately 22-23 days, after which time the proportion of observations in which the nest was attended began to decrease and the rate of visits to the nest increases (Figure 2.12). Based on this assumption of 22 days incubation, fledging periods ranged from around 37 to 49 days after hatching; no significant variation in the length of the fledging period was found among nesting seasons ($F_{3,11}$ = 1.03; P = 0.417; Figure 2.13). The time between hatching and fledging did not vary between nesting attempts producing one, two and three fledglings when data were combined among territories and seasons ($F_{2,12}$ = 1.59; P = 0.244; Figure 2.14). Insufficient data were available for comparisons in fledging period among territories (Figure 2.15).

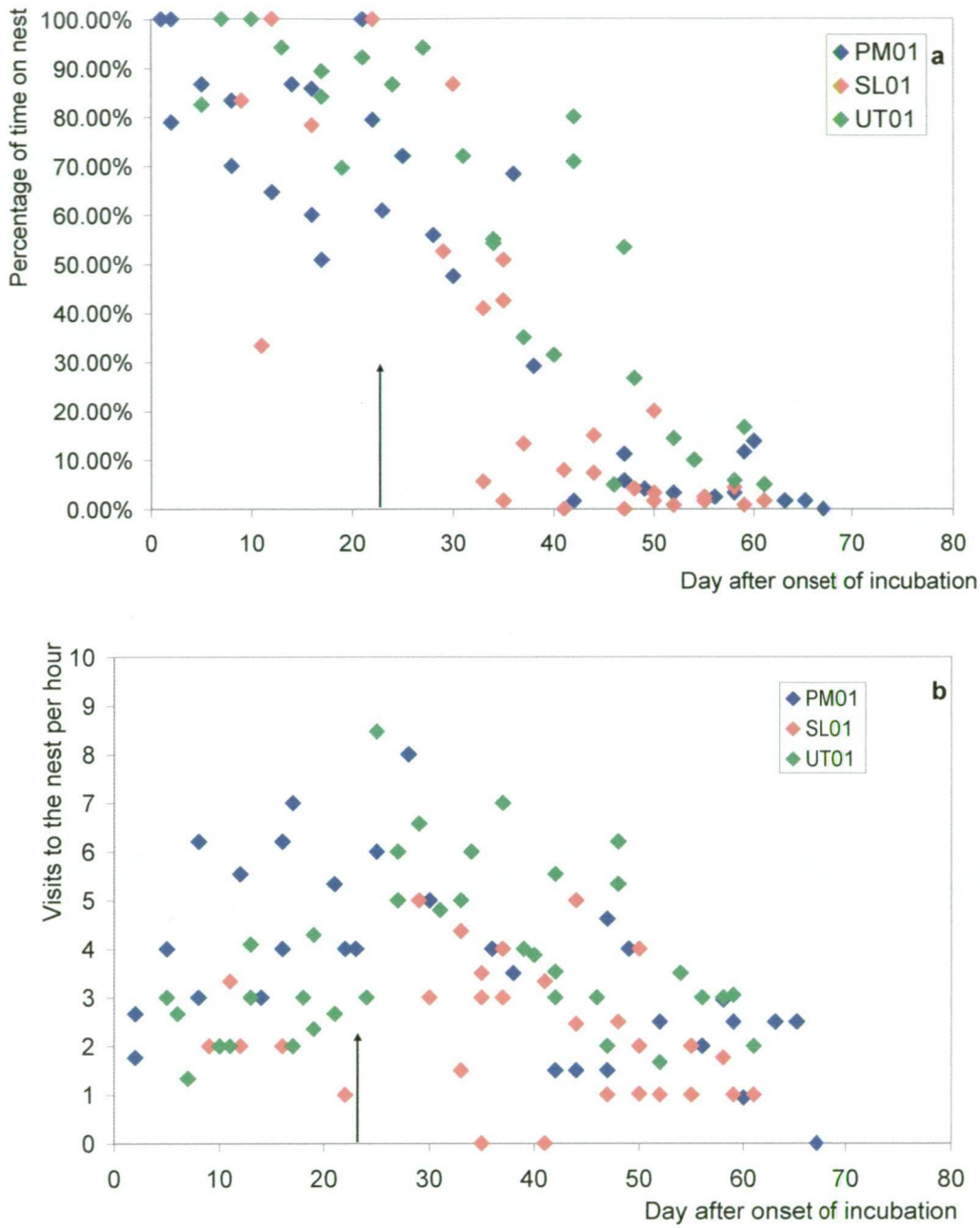


Figure 2.12 Proportion of observations in which the nest was attended (a) and visits to the nest per hour (b) relative to time after onset of incubation in Forest Ravens. Arrows indicate assumed approximate time of hatching around day 23

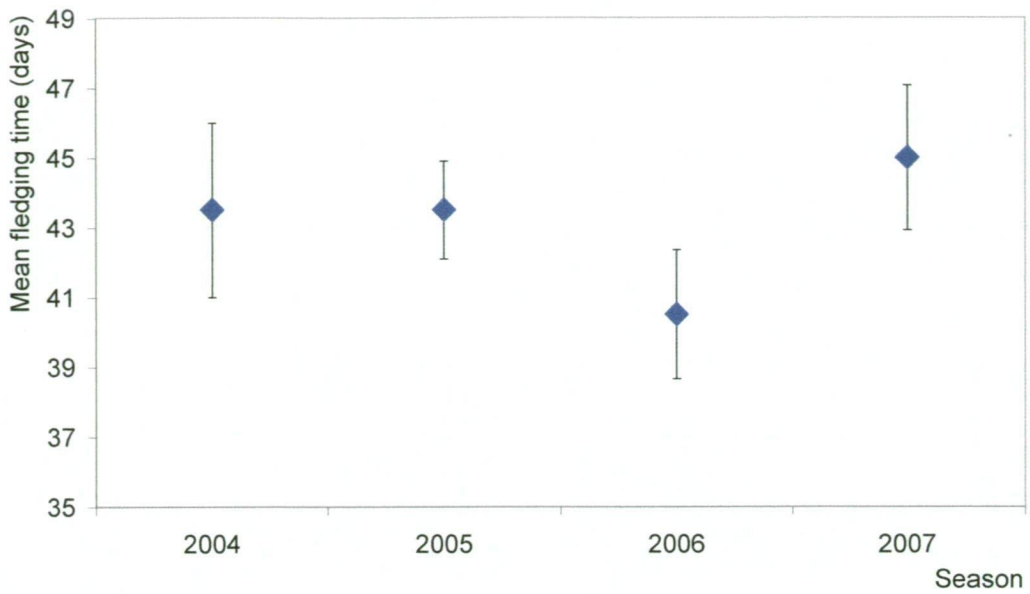


Figure 2.13 Estimated time (mean ± SE) between hatching and the flight of the first fledgling from the nest tree for Forest Ravens across four breeding seasons.

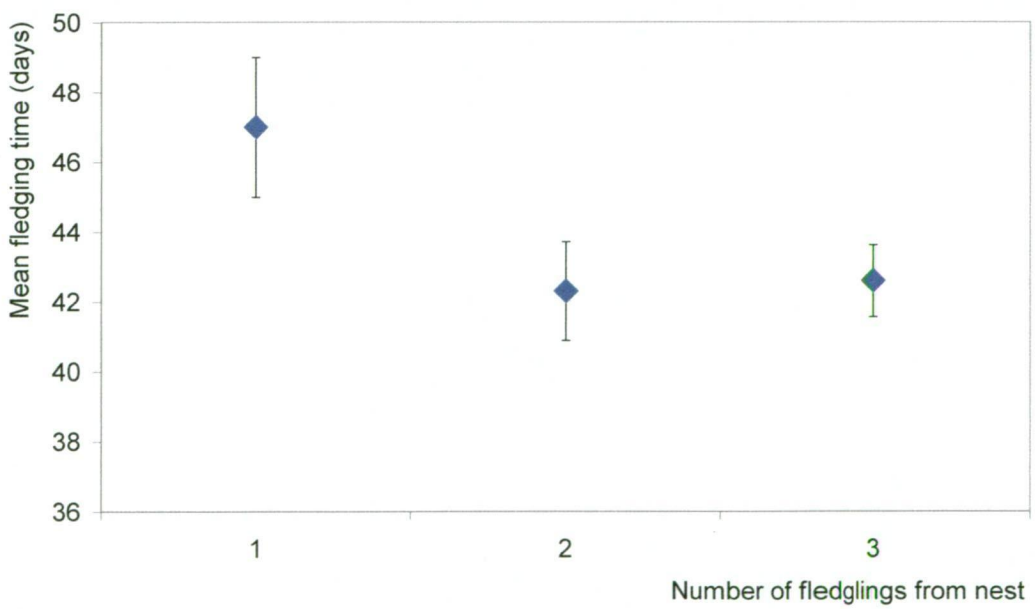


Figure 2.14 Estimated time (mean ± SE) between hatching and the flight of the first fledgling from Forest Raven broods producing 1, 2 and 3 fledglings. Data combined from six territories over four breeding seasons.

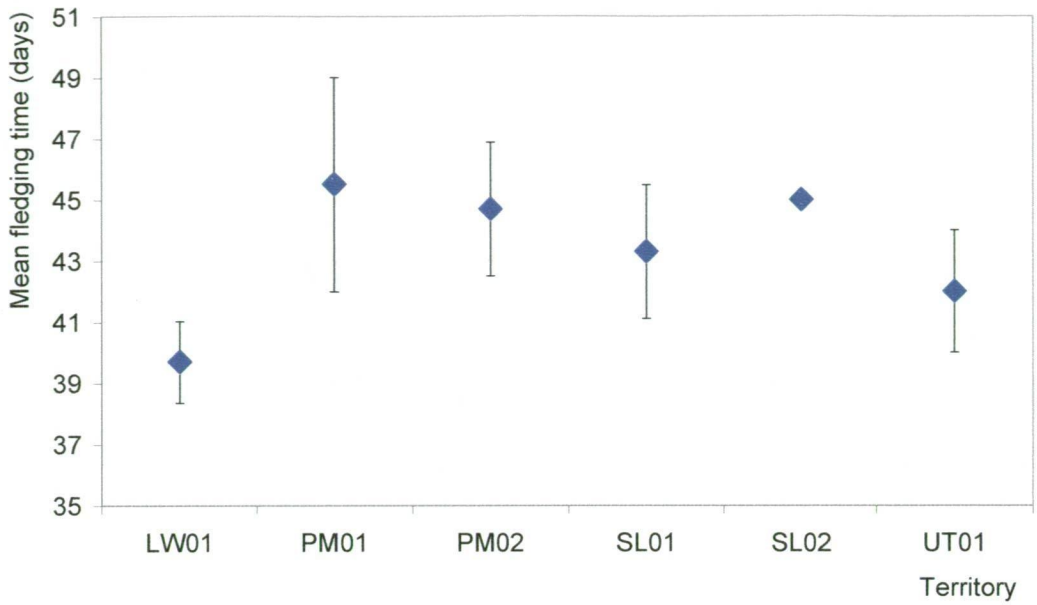


Figure 2.15 Estimated time (mean ± SE) between hatching and the flight of the first fledgling from the nest tree for Forest Ravens across six territories. Data combined across four breeding seasons

Fledging

The fledging process for Forest Ravens was gradual, and the exact time at which an individual finally left the nest was difficult to ascertain. There were a number of stages in the fledging process, the duration of which vary somewhat between individuals:

1. Approximately two weeks before leaving the nest: nestlings began to stand up in the nest, flapping or stretching their wings and preening.

2. Approximately one week before leaving the nest: nestlings spent time standing on the nest rim, initially prior to or following parental visits but eventually with no apparent stimulus. The time spent on the nest rim increased gradually, but varied between a couple of seconds and some minutes. The fledgling still flapped

and stretched its wings, preened, and also pecked and pulled at twigs and leaves in and around the nest.

3. Approximately three days before leaving the nest: the fledgling began to spend some time outside the nest. The time spent outside the nest increased gradually; initially the fledgling appeared very tentative leaving the nest, and made several attempts before remaining next to the nest for more than a couple of seconds: the third SL01 fledgling of 2006, for example, leapt in and out of the nest seven times, barely touching the branch before leaping back in, and similarly barely landing in the nest before leaping back out, before it managed to remain for more than a few seconds outside the nest.

4. Approximately two days after leaving the nest: the fledgling made its first flight out of the nest tree. After this it appeared that the fledgling did not return to the nest.

Forest Raven brood-mates fledged asynchronously. Where two nestlings survived to fledging, the first fledged on average 2 days before its sibling (0-4 days, $n = 8$ broods). In broods of three the first fledged on average 3 days (0-6 days, $n = 5$ broods) before the remaining two, which fledged together.

2.3.4 Parental care

Parental care observed at the nest by Forest Ravens in this study included incubation of eggs, brooding of young nestlings, provisioning of nestlings from hatching to fledging, and cleaning of the nest.

Nest attentiveness

Overall, Forest Raven eggs were incubated for 83.1% of observation points (observation points at 30-second intervals) during daylight hours. In individual observation bouts the proportion of observations in which the nest was covered

ranged from 57% to 100%. Analysis of variance performed on the data, using all territories combined but with territory as a random factor, indicated that the proportion of time spent on the nest during incubation did not vary significantly between morning and afternoon ($F_{1,1} = 3.72$; $P = 0.304$). The proportion of time spent on the nest decreased significantly between incubation and the first two weeks after hatching only in the UT01 ravens (Table 2.6).

Table 2.6 Two-tailed t-tests comparing percentage of observations in which Forest Raven nests were attended between incubation (Stage 0) and the first two weeks of brooding (Stage 1)

Territory	*Stage 0 mean % (SE)*	*Stage 1 mean % (SE)*	*d.f*	*t-stat*	*P(T<=t) two-tail*
PM01	80.0 (0.04)	77.1 (0.08)	21	0.36	0.724
SL01	79.0 (0.12)	46.5 (0.50)	9	2.09	0.066
UT01	89.3 (0.03)	64.3 (0.16)	9	2.70	0.024*
All territories	83.1 (0.03)	63.5 (0.06)	31	3.19	0.003*

During incubation the nest was unattended on average 1.8 times per hour ($n = 33$ observation bouts; SE = 0.26; 0-4); mean absence duration was 5.6 minutes ($n = 49$ absences; SE = 0.45; 1-23min). Incubating ravens left the nest to chase other ravens from the nest area, followed the partner off the nest after a feeding visit or after the partner called from nearby, or left spontaneously to feed, preen or defecate.

As individual parents could not be identified it was not possible to determine which was on the nest at any given time. Twice during the brooding phase (UT01; PM01) a cross-over was observed, where a brooding raven was visited by its mate; after feeding, the brooding bird left the nest and the nest was covered by the second bird. This indicates that to some extent both males and females undertake

brooding behaviour, although when two ravens were seen together in this study it appeared that only one had developed a brood patch. In a third observation (PM01), a visiting bird stood over the nest while the other, which had been brooding, was absent; at the time a pair of Brown Falcons (*Falco berigora*) were flying around in the vicinity of the raven nest.

During the nestling phase the proportion of observations in which the nest was attended decreased as the nestlings aged. Analysis of covariance on linear regressions for each nest found no significant difference among breeding seasons in the SL01 ravens (2005-7) or the PM01 ravens (2005, 2007) (Table 2.7; Figure 2.16; Figure 2.17). In the UT01 ravens nest attendance followed a similar decrease among all nesting seasons (2005-7) but was lower in 2006 than in 2005 or 2007, which were not significantly different from each other (Table 2.7; Figure 2.18).

When years were combined as appropriate, ravens from the three territories did not show significant differences in the slope of the regression lines but did vary significantly in their intercepts, with the UT01 ravens spending the most time on the nest and the SL01 ravens the least (Table 2.17; Figure 2.19).

Table 2.7 Analysis of covariance and linear regression for proportion of observations in which Forest Raven nests were attended (PTON) relative to day after hatching (DAH). Comparisons between seasons (within pairs) and between pairs. Data are arcsine transformed.

Compared variables	*P (homogeneity of slopes)*	*Common slope*	*Intercept (adjusted to common slope)*	*P (Intercept)*	*r2*	*Significance of r2*
PM01 2005 PM01 2007	0.1672	-0.0228	0.9006 0.8221	0.8870	0.695	P<0.0001
SL01 2005 SL01 2006 SL01 2007	0.5754	-0.0176	0.6439 0.5746 0.6601	0.7064	0.438	P=0.0004
UT01 2005 UT01 2006 UT01 2007	0.5346		1.1799 0.7390 1.0864	0.0017*	0.538	P<0.0001
UT01 2005 UT01 2007	0.5528	0.0284	1.2322 1.1290	0.4218	0.732	P<0.0001
UT01 2006	-	-0.0270	0.7390	-		
PM01 (2005,7) SL01 (2005,6,7) UT01 (2005,7)	0.2371	-0.0190	0.8895 0.7359 1.0212	0.0004*	0.591	<0.0001

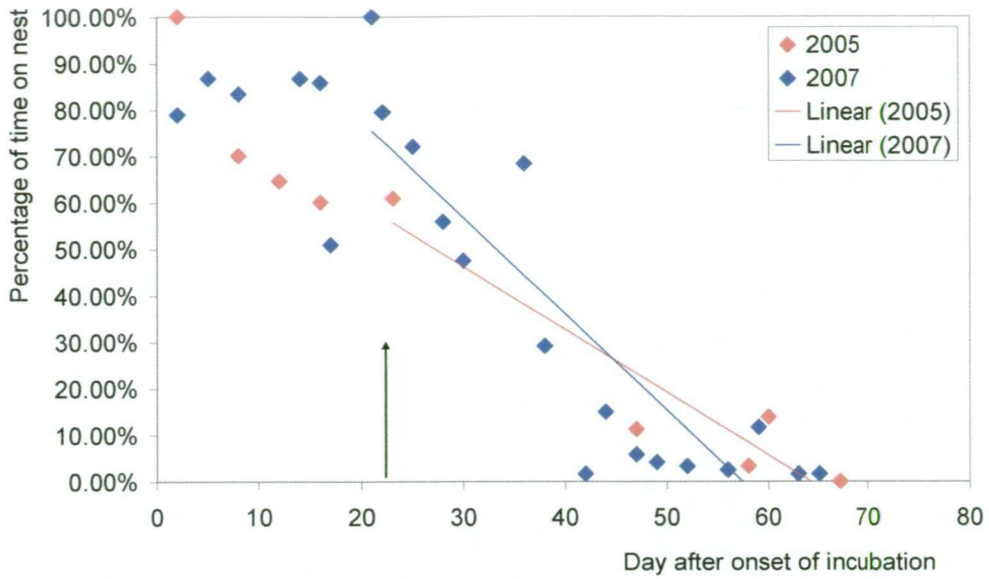


Figure 2.16 Percentage of observations in which the nest was attended in the PM01 territory relative to time after the onset of incubation, 2005 and 2007 nesting seasons. Arrow represents approximate time of hatching. Trendlines reflect post-hatching data only. Data were arcsine transformed for analysis. See Table 2.7

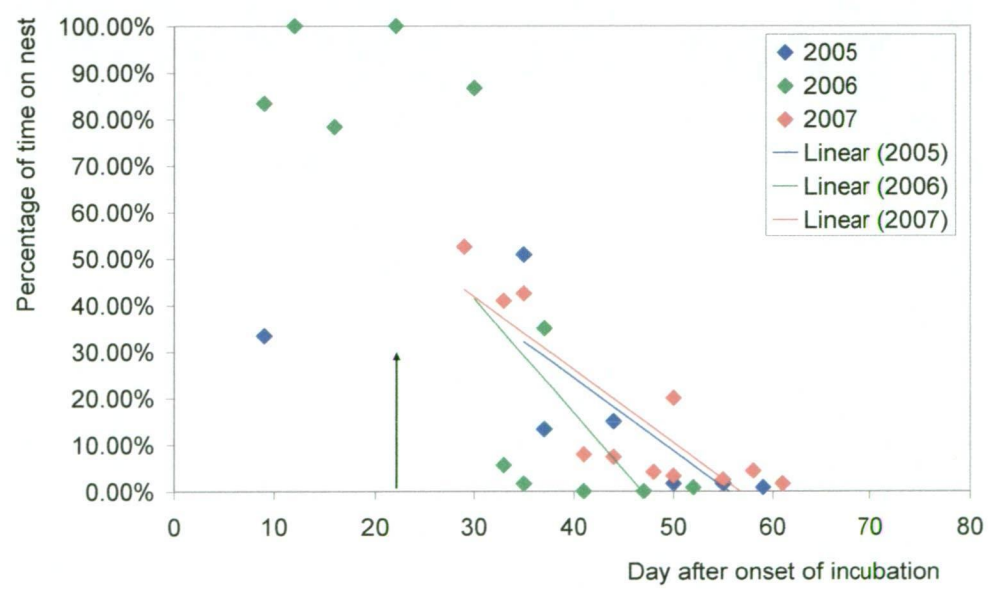


Figure 2.17 Percentage of observations in which the nest was attended in the SL01 territory relative to time after the onset of incubation, 2005 and 2007 nesting seasons. Arrow represents approximate time of hatching. Trendlines reflect post-hatching data only. Data were arcsine transformed for analysis. See Table 2.7

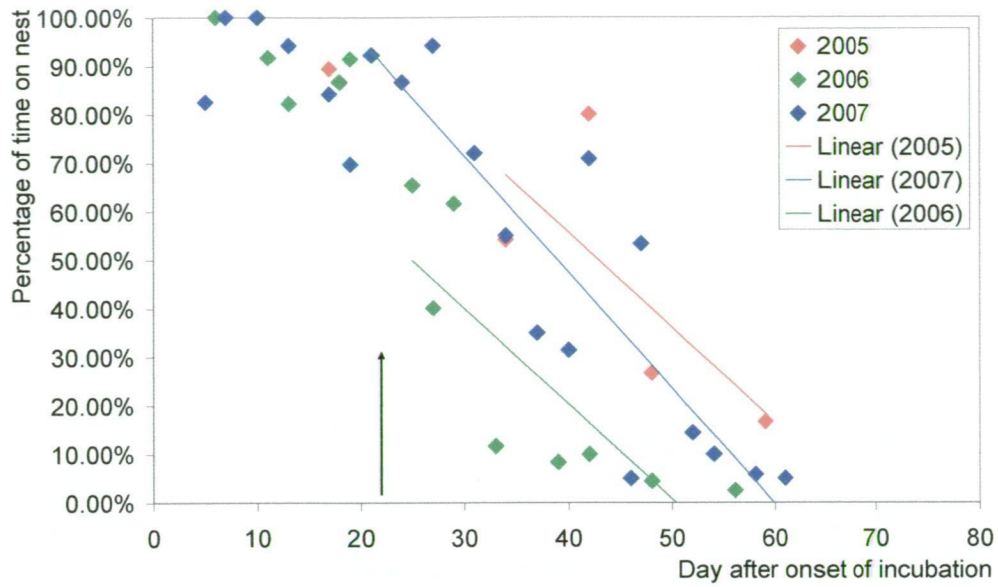


Figure 2.18 Percentage of observations in which the nest was attended in the UT01 territory relative to time after the onset of incubation, 2005 and 2007 nesting seasons. Arrow represents approximate time of hatching. Trendlines reflect post-hatching data only. Data were arcsine transformed for analysis. See Table 2.7.

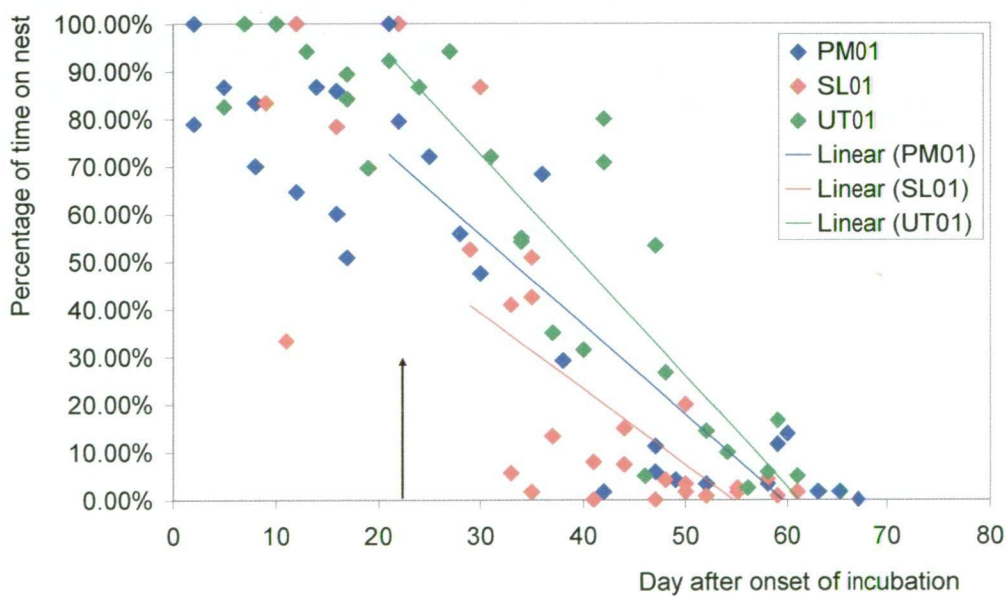


Figure 2.19 Linear regression of the percentage of observations in which the nest was attended relative to time after onset of incubation in three Forest Raven territories. PM01: 2005, 2007; SL01: 2005, 2006, 2007; UT01: 2005, 2007. Trendlines reflect post-hatching data only. Data were arcsine transformed for analysis. See Table 2.7

It was found that the decrease in nest attendance over time followed an exponential decay curve of the form:

proportion of observations in which nest is attended = α exp (-β*days after hatching)

The values of α and β for individual pairs are given in Table 2.8. Figures 2.20, 2.21 and 2.22 show the fitting of these models to the data.

Table 2.8 Values of alpha and beta best describing the exponential decay curve of nest attendance over time in three Forest Raven territories.

Territory	*Seasons included in model*	*α (± SE)*	*β (± SE)*
PM01	2005, 2007	0.9712 ± 0.079	0.0720 ± 0.010
SL01	2005, 2006, 2007	2.5256 ± 1.087	0.1471 ± 0.035
UT01	2005, 2007	1.0853 ± 0.137	0.0457 ± 0.009
All territories	as above	1.0393 ± 0.088	0.0677 ± 0.007

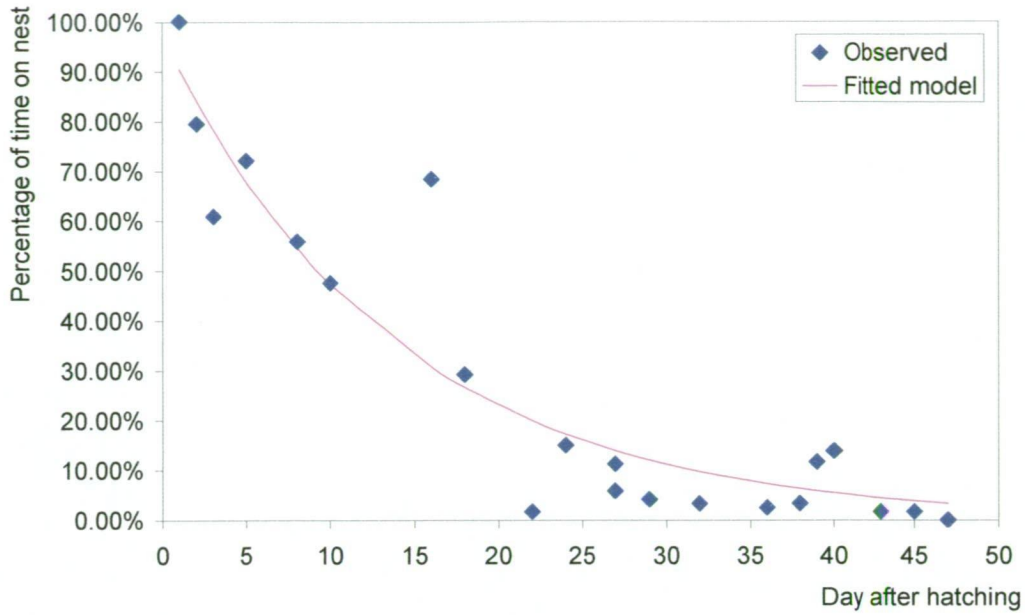


Figure 2.20 Non-linear regression model showing the percentage of observations in which the nest was attended relative to the time after hatching in the PM01 territory, for nesting seasons 2005 and 2007

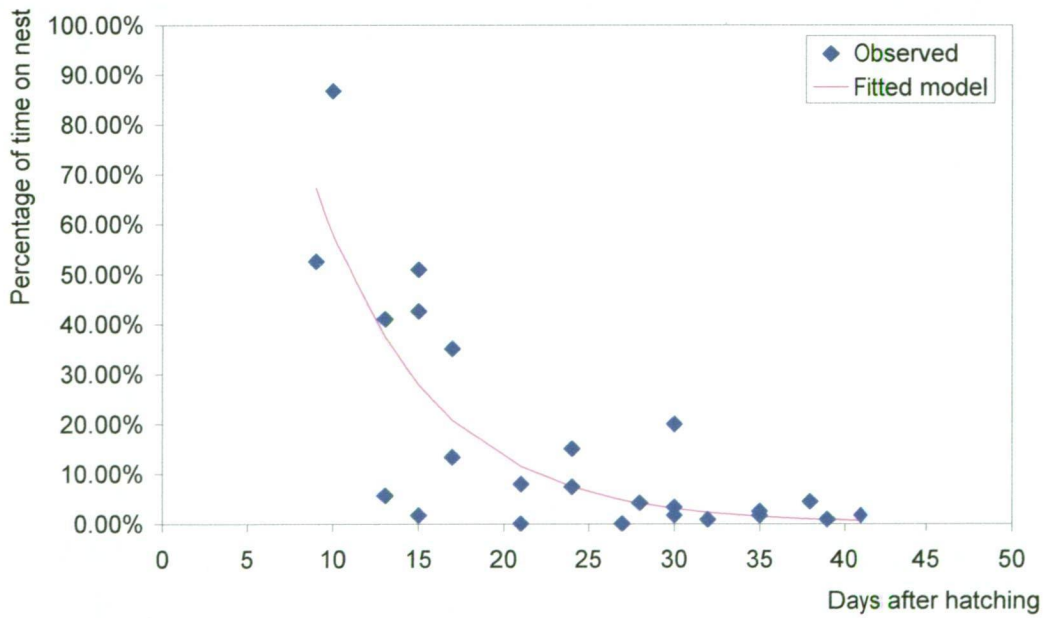


Figure 2.21 Non-linear regression model showing the percentage of observations in which the nest was attended relative to the time after hatching in the SL01 territory, for nesting seasons 2005 and 2007

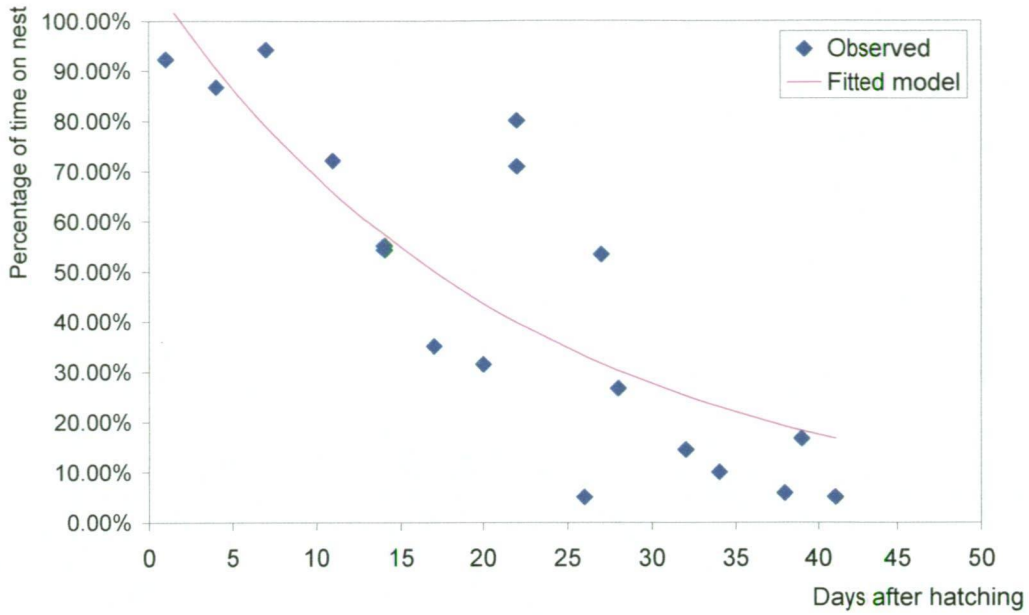


Figure 2.22 Non-linear regression model showing the percentage of observations in which the nest was attended relative to the time after hatching in the UT01 territory, for nesting seasons 2005 and 2007

Visits to the nesting raven

Ravens on the nest incubating or brooding were fed by their mate. The frequency of this varied among pairs. The incubating SL01 bird was not visited on the nest at all in 4.8 hours of observations, while the incubating PM01 and UT01 birds were visited on the nest seven times in 11.7 hours (0-4 times per hour), and 14 times in 12.3 hours (0-5 times per hour), respectively.

Provisioning of nestlings

Both parents were involved in provisioning nestlings from the time of hatching. Early in the nestling period one adult brought food to the nest while the other brooded, but later both adults brought food to the nest. When both adults arrived at the nest tree together, one would wait until the other had fed the nestlings and left before approaching the nest. The frequency of visits to the nest increased

between incubation and the first two weeks of brooding as food was provided for the nestlings as well as the brooding adult; two-tailed t-tests were significant at α=0.05 for all territories combined and for the SL01 territory alone (Table 2.9).

Table 2.9 Two-tailed t-tests comparing number of visits per hour to Forest Raven nests between incubation (Stage 0) and the first two weeks of brooding (Stage 1)

Territory	*Stage 0 mean (SE)*	*Stage 1 mean (SE)*	*d.f*	*t stat*	*P(T<=t) two-tail*
PM01	3.90 (0.44)	5.23 (0.55)	21	-1.75	0.094
SL01	2.07 (0.37)	3.73 (0.35)	9	-3.24	0.010*
UT01	3.61 (0.94)	5.28 (0.75)	18	-1.49	0.153
All	3.52 (0.41)	4.84 (0.42)	53	-2.49	0.016*

Over the period from hatching to fledging there was a significant linear decrease in the number of visits to the nest, although considerable scatter about the line was seen in all pairs. Analyses of covariance found no significant difference in the slope or intersect of the data among years in the SL01 or the UT01 territories (Table 2.10; Figure 2.23; Figure 2.24). 2006 data were not included for the PM01 territory due to abnormal results from failed nests in Stage 2. In this territory both the slope and the intersect differed between 2005 and 2007 (Table 2.10; Figure 2.25), with the rate of visits in 2005 higher in the early stages of the nestling period, decreasing more rapidly to end at a lower visiting rate than in 2007. When annual data were combined ravens from the UT01 and SL01 territories exhibited an equal rate of decrease in nest visits over time (slope), but significantly different intercepts (Table 2.10) with the UT01 adults tending to visit the nest more often than the SL01 adults throughout the nesting period (Figure 2.26).

Table 2.10 Analysis of covariance and linear regression for the number of visits to the nest per hour (VTN) relative to day after hatching (DAH). Comparisons between seasons (within pairs) and between pairs

Compared variables	*P (homogeneity of slopes)*	*Common slope*	*Intercept (adjusted to common slope)*	*P (Intercept)*	*r2*	*significance of r2*
PM01 2005 PM01 2007	0.026*	-0.099	6.468 5.877	0.436	0.567	<0.001
SL01 2005 SL01 2006 SL01 2007	0.736	-0.071	3.826 4.149 5.183	0.112	0.215	0.023
UT01 2005 UT01 2006 UT01 2007	0.769	-0.077	5.584 5.737 6.103	0.796	0.265	0.007
SL01 (2005,6,7) UT01 (2005,7)	0.868	-0.088	4.055 5.947	<0.001*	0.250	<0.001

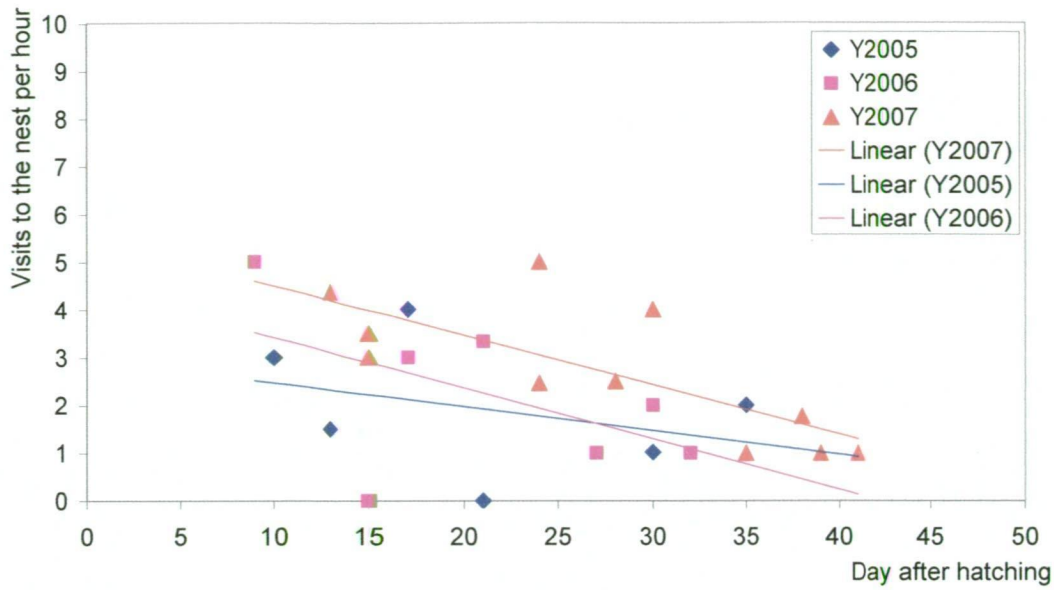


Figure 2.23 Linear regression of the number of visits to the nest per hour relative to the time after hatching in the UT01 territory, 2005, 2006 and 2007 nesting seasons. See Table 2.10 for analysis.

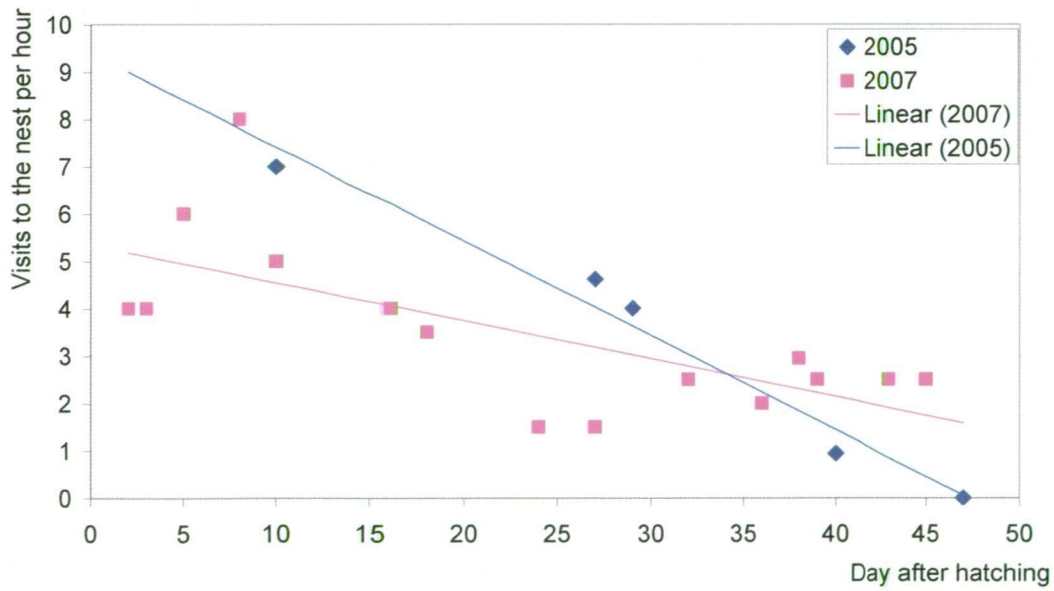


Figure 2.24 Linear regression of the number of visits to the nest per hour relative to the time after hatching in the SL01 territory, 2005, 2006 and 2007 nesting seasons. See Table 2.10 for analysis.

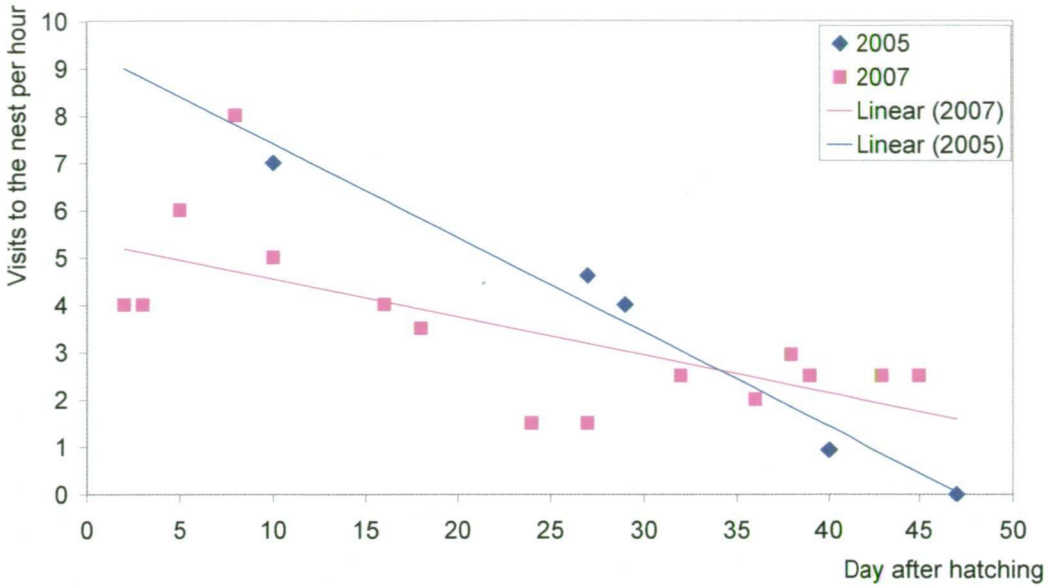


Figure 2.25 Linear regression of the number of visits to the nest per hour relative to the time after hatching in the PM01 territory, 2005 and 2007 nesting seasons. See Table 2.10 for analysis.

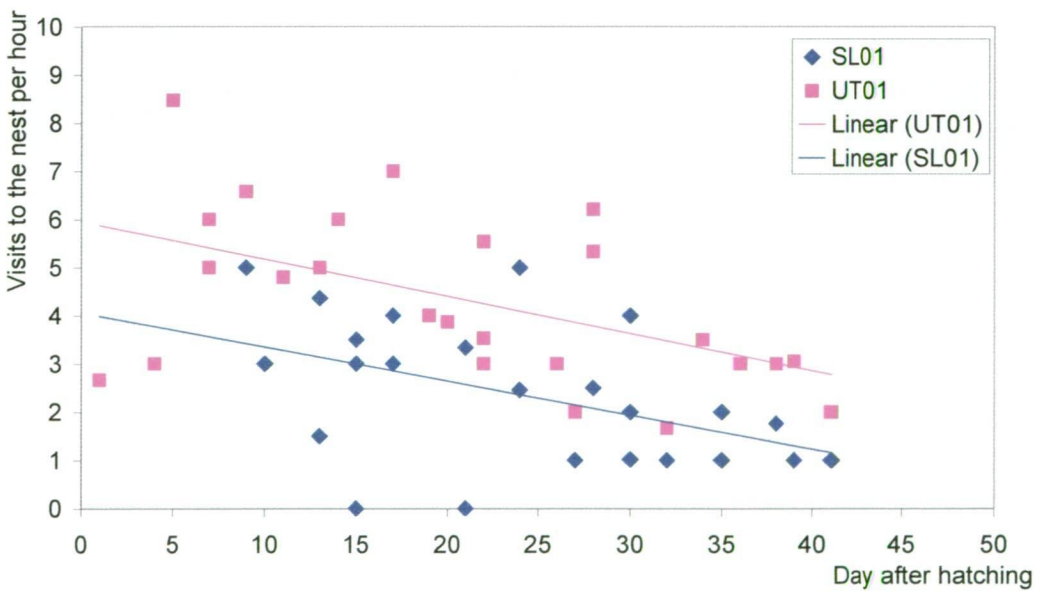


Figure 2.26 Linear regressions of the number of visits to the nest per hour relative to the age of nestlings in the UT01 and SL01 territories. See Table 2.10 for analysis.

Two-tailed t-tests on the data from all nests combined indicated that the number of visits to the nest per hour did not vary significantly between morning (Time 1; 5.01 visits/hour; SE = 0.48) and afternoon (Time 3; 4.63 visits/hour; SE = 0.29) in the first two weeks after hatching (*d.f.* = 17; $t = 0.58$; $P = 0.570$). Insufficient data were available for comparisons with Time 2.

Nest sanitation

Both parents were involved in nest sanitation. Faecal sacs were removed after nestlings were fed; the sacs were either picked from the wall of the nest, or taken directly from the cloaca of the nestling as they were produced. This occured up to the time of fledging. By the fifth week after hatching, nestlings were able to defecate over the edge of the nest, requiring the adults to also clean the outside of the nest. At this stage, the outside of the nest became whitened; later, when nestlings were able to stand on the nest rim, the ground below the nest became heavily whitewashed. Some nest cleaning by parents still occured at this stage.

Faecal sacs were either consumed by the adults or taken away in the beak. No data could be collected on the frequency of these behaviours, but observations suggested an early tendency towards consumption of faecal sacs, while later in the nestling period more faecal sacs were taken away. In the PM01 ravens faecal sacs removed from the nest were taken to nearby trees, where they were then smeared on a branch.

Nest cleaning behaviour, characterised by a head-down-tail-up position and much tail-shaking, was also seen during incubation, suggesting that insects and other parasites may also have been removed from the nest at this time and during the nestling period. Incubating birds left the nest to defecate.

Provisioning of juveniles

Juvenile Forest Ravens exhibited adult-style foraging techniques, such as pulling at leaves and probing under bark, from the time they left the nest, although the it is not known how effective these behaviours were. Provisioning of juveniles by adults was seen up to two months post-fledging, although by this time most begging attempts were unsuccessful, and parents became aggressive towards persistent juveniles.

Provision of food to juveniles took three forms: quick visits in which a single item of food was provided; longer visits in which juveniles were fed a number of times in succession either from a large food item or on food collected there; or juveniles were led to a food cache to feed themselves. As when in the nest, juvenile Forest Ravens were fed on both natural and anthropogenic food sources, including fruit (such as apple cores), bread, carrion, insects, small animals and plant materials.

2.4 Discussion

Little is known about the nesting period of Forest Ravens in Tasmania. Recent studies of nesting pairs of Northern Forest Ravens in New South Wales have recently been undertaken by Secomb (2005) and Debus and Rose (2006), and the breeding biology of the Australian Raven has been comprehensively studied by Rowley (Rowley, Braithwaite *et al.* 1973; Rowley 1973c). This study investigated breeding season, productivity, nest success and re-nesting behaviour of Forest Ravens in southern Tasmania. The results suggest that, as assumed, close similarities exist between the subject ravens and the Australian Raven and Northern Forest Raven of the Australian mainland.

The few published studies of Northern Forest Ravens have included few pairs (e.g. four pairs, Debus and Rose 2006; one pair, Secomb 2005b) and have lasted only short periods. The majority of the available breeding data for Forest Ravens and Northern Forest Ravens have been collected by amateur bird-watchers,

published in local ornithological journals, and collated in Higgins *et al.* (2006). Despite the small number of data points available from the Nest Record Scheme and other sources, given the dearth of published studies of Forest Raven and Northern Forest Raven breeding biology such references form a significant part of the current knowledge of the species. Although use of collated nest record data has disadvantages such as a potential bias towards easily-located and early nesting attempts (Holyoake 1967), the importance of amateurs in ornithology has been recognised by a number of authors. Ornithology is a field in which "profound knowledge or elaborate equipment" (Mayfield 1979) is not required for the collection of basic data; the qualifications of many amateur ornithologists, while not formal qualifications, come through extensive field work and experience (Greenwood 2007). As such, data obtained by non-professional or non-academic researchers should be recognised as useful additions to the body of knowledge regarding bird species. Clarke (1997) argues for the importance of amateur ornithologists in the collection of data for bird species which may not be suitable study species for scientific or academic researchers looking for large, publishable data sets. Such species include those with large home-ranges or those that breed non-colonially or non-cooperatively (Clarke 1997). The Forest Raven fits these criteria: pairs nest non-colonially, once a year, in territories said to be up to 40 hectares in size (Rowley 1973c). Although Clarke (1997) discusses only the Australian research climate, many of the corvid studies available from the northern hemisphere also involve cooperatively-breeding populations (e.g. Carrion Crows, Baglione *et al.* 2002, Richner 1990; American Crows, Chamberlain-Auger *et al.* 1990), while for other species large amounts of data from sources ranging from scientific papers to amateur ornithologists have been collated by professional or academic ornithological researchers (e.g. Holyoake 1967; Ratcliffe 1997; Marzluff and Angell 2005).

While the data available from sources such as the Nest Record Scheme and from local ornithological journals are important, they are not ideal for comparisons, largely comprising individual, opportunistic observations. However, there should be little doubt as to the accuracy of the data: these observations are usually

restricted to objective, quantitative data such as clutch sizes, brood sizes and the timing of breeding. The data presented in collated sources such as Higgins *et al.* (2006) generally fall within a small range of values, indicating that the findings of amateur ornithologists are consistent with, and therefore equally useful as, those from scientific or academic sources. Finally, contributions to local journals are not indiscriminate, but tend to be reviewed by experts with high levels of local knowledge (Knight *et al.* 2008). Despite this, the potential for bias in opportunistic data collected by amateurs (Holyoake 1967) supports the need for more planned and long-term studies of species such as the Forest Raven, whether by academic or amateur researchers.

2.4.1 The nest

Forest Raven nest characteristics, construction behaviour and nest-site selection have been to some extent previously recorded (Higgins *et al.* 2006). The results of this study support, and add to, existing knowledge of nesting in the species. Overall, nesting in the Forest Raven is consistent with that of other ecologically similar corvid species.

Nest location

The selection of an appropriate site in which to build a nest may depend on several factors which regulate both the broad area in which a nest site is selected and the final position of the nest itself. Such factors may include climate, predation risk, the availability of food and nesting materials, and accessibility of the nest to the parent birds (Hansell 2000). The means by which these factors are addressed depend on characteristics of the local vegetation. This study focussed on nest height, branching order, and the height of the nest tree relative to surrounding trees as potential influencing factors in Forest Raven nest-site selection. While the nest sites selected by ravens in this study did imply some preferences in these factors, Forest Raven territories were large and contained large numbers of potential nest trees matching these criteria; it was impossible to

tell from a study of this size whether seemingly appropriate nest sites were selected randomly or whether other physical factors determined nest site selection in the species.

Thirty-five Forest Raven nests in this study were located an average of 23.7 m above the ground, ranging in height from 10 m to 39 m. Green (1995) found Forest Raven nests ranging between seven and 30 m above the ground, while other records of nests give a height range of three to 35 m above the ground (Higgins *et al.* 2006). Nest heights reflected the height of the local vegetation, as could be seen in the relative consistency in nest heights within individual and neighbouring territories, as opposed to the large discrepancy among territories: for instance, nests used by the SL01 ravens ranged from 34 m to 39 m, while those in the PM01 and PM02 territories ranged from 19 to 23 m above the ground. As the number of Forest Raven territories included in this study was small, the results potentially reflect nest height preferences of ravens within each particular territory, however the observed results were consistent with a broad-scale correlation between nest height and habitat: lower nests were found in the Tasmanian midlands, which are characterised by sparse, low trees scattered in agricultural grasslands, than in the semi-suburban light bushland found in much of southern Tasmania. Similarly, McGowan (2001) found that American Crow nests in suburban areas tended to be placed significantly higher and in taller trees than those in rural areas, again as a result of the available nest sites in each area.

The majority of Forest Raven nests observed were located in third-order branchings of Eucalyptus trees, although as individual pairs varied in their nest positioning it is uncertain that this reflected a true preference. A nest must be placed in branches which are strong enough to support the nest itself as well as a number of large nestlings and at least one adult; this would also determine the minimum tree size in which a nest could potentially be built. No data could be obtained on the weight of Forest Raven nests, however they are likely to be similar to those of the Australian Raven, which weigh on average more than 3.5 kg (Higgins *et al.* 2006). While lower order branchings provide stronger branches

upon which a nest can be placed, proximity to the trunk of the tree may increase the risk of predation by climbing animals. Although mammalian predation of Forest Raven nests has not been reported, Common Brushtail Possums (*Trichosurus vulpecula*) and introduced Black Rats (*Rattus rattus*) are both known to climb trees and to eat meat and, in the case of the rat, eggs (Green Undated). No nests were located in the top of the nest-tree canopy; while few were located in the canopy the majority of nests were built below the canopy. This may have been due to the physical limitations of thin canopy branches, but is also likely to reduce the visibility of nests from the sky and therefore the potential for eggs and nestlings to be located by aerial predators. Foliage above the nest may provide a thermal benefit to nestlings or the incubating adult through reduction of solar radiation or heat loss (Walsberg and King 1978a; Wachob 1996).

As for the Australian Raven (Higgins *et al.* 2006), it appeared that the nest sites of Forest Ravens were chosen in part for their view of the surrounding area. As nesting ravens regularly turned on the nest, facing in various directions within a single incubation bout, it is likely that nest sites provided a wide view over the nest area, allowing early detection of potential threats from all directions. Again, the local vegetation determined how this was achieved. In areas of relatively dense vegetation the nest was usually in the tallest tree within at least 20 metres, and in many cases the nest was located above the canopy of nearby trees. Nest trees were often, but not always, located on the edge of a patch of bush. The majority of nests in light bushland areas were located in the top eighth of the nest tree. In areas of more sparse vegetation nests were often located in trees standing alone; when located in a tree which was surrounded by others as a clump, nests were situated below the canopy of the surrounding trees, allowing a clear view through the bare branches. In this habitat type the majority of nests were located in the lower top quartile of the nest tree. In both dense and sparse vegetation, nest trees were characteristic of the tallest vegetation in the general area. The findings of this study are consistent with a study of nest site selection in Northern Ravens (Dunk *et al.* 1997), in which the authors suggested that construction of nests in isolated stands of trees or on the edges of larger stands, most often in the tallest

tree within the plot, provided visibility of potential predators and/or food sources (Dunk *et al.* 1997). Such positioning, along with the siting of nests in outer branches, also allows increased accessibility to the nest for the parents (Dunk *et al.* 1997) and may reduce damage to feathers caused by passing through dense vegetation (Cresswell 1997); however, increased nest accessibility through a reduction in surrounding foliage may also increase predation risk and therefore reduce nest success (Holyoake 1967; Martin 1993). Cresswell (1997) found that parental behaviour mitigated the risk of predation from poorly concealed Blackbird (*Turdus merula*) nests. While no nest predation was observed at Forest Raven nests in this study, ravens were seen to act aggressively towards intruders into the nest area; this, combined with the high level of nest attentiveness of the ravens (this study) suggests that Forest Ravens are likely to be strongly defensive of the nest and nest concealment may be of relatively little importance to the species. This would be of particular value in areas of sparse vegetation, such as the Tasmanian midlands, where potential nest sites are few and are therefore more conspicuous than in areas with more trees (Martin 1993).

Forest Ravens, and other corvid species, are able to nest in a range of habitats, tree forms and other nest sites (Higgins *et al.* 2006). This flexibility suggests that changes in land use, such as increasing vegetation clearance for agriculture and urbanisation, would have little impact on their ability to find an appropriate nest site. In this study nest height, location and nest tree characteristics were apparently determined by habitat; although Forest Ravens appeared to select nest sites according to a number of physical criteria, further studies into reproductive success of the species are required to determine whether these choices are adaptive.

Nest characteristics and construction

Forest Raven nests in Tasmania were found to be very similar to descriptions of Australian Raven nests found on the Australian mainland (Rowley 1973c) and

tree nests of the Common Raven in Britain (Ratcliffe 1997) and North America (Heinrich 1999).

Forest Raven nests were built or repaired in late winter or early spring, with a peak in construction behaviour occurring in mid- to late August. Nest construction or refurbishment took place over several days, up to approximately two weeks. Nests were completed within one month of laying, although the timing of observed nesting behaviour among pairs was more variable than the timing of laying. The timing of nest construction or refurbishment did not affect the timing of laying: the majority of first nesting attempts began in September, and the time between nest construction and the onset of incubation was significantly greater when construction was observed in August than in September.

Second clutches were laid sooner after the completion of the nest than first clutches, most likely due to the urgency of raising a brood before the end of the optimum breeding season. One explanation for the re-use of nests by birds is that renovating a nest takes less time than building a new one, and therefore allows for earlier laying (Hansell 2000), which in turn may increase nest productivity (Ignatiuk and Clark 1991; Dunk *et al.* 1997). Contrary to this, whether a new nest was built or an old one refurbished did not affect the timing of breeding in Forest Ravens.

In one case seen in this study a nest was apparently built in late summer or early autumn. This may form evidence of autumn sexuality, a phenomenon seen in some photoperiodic species whereby slight gonadal recrudescence and sexual behaviour occurs at this time as a result of the end of the photorefractory period combined with appropriate day-lengths (Lofts and Murton 1968). This has been reported in Rooks (Marshall and Coombs 1957), but is extremely rare in Australian Ravens, in which the only reported evidence is the building of a nest in May (Rowley, Braithwaite *et al.* 1973). The early nest found in this study, as with that found by Rowley, was renovated at the usual time, before laying occurred. Rowley (1973c) found that in some years with good autumn rain Australian

Raven nests were begun in May and not completed until July. Some birds continue to construct the nest after the first egg has been laid (Hansell 2000); in 2007 the PM01 ravens in the current study were seen to add sticks to the wall of the nest around the time of hatching.

As with most corvid species (Goodwin 1977), both male and female Forest Ravens were involved in nest construction. This is a common feature of socially monogamous, non-passerine species, but the role of males at this time is more variable in passerine species (Ligon 1999). Male contribution to nest construction may be particularly important in species with large nests: in the Carrion Crow, the energetic cost of building a nest is equivalent to that of the production of 2.7 clutches (Hansell 2000), so sharing this cost reduces the strain on one member of the pair. The time spent in constructing a nest is also a major cost to the breeding bird, as increased nest productivity may occur as a result of earlier laying (Hansell 2000). Again, this may be mitigated by both members of a pair being involved in stick-collection and construction. Soler *et al.* (1998) suggest that investment in reproduction is increased in species in which both sexes build, as each nest construction allows each member of the pair to assess the quality of the other. As Forest Ravens usually mate for life, it is uncertain that this theory would apply.

As ravens were not banded in this study, it was impossible to determine whether each member of a pair had certain roles; certainly both collected sticks and incorporated them into the nest wall. It appeared that only one member of the pair at a time was involved in forming the lining of the nest, although the other member brought lining material to the nest. It may be assumed that it was the female who shaped the nest lining, as a close fit between the incubating bird and the edge of the nest is important for insulation of the eggs (Rowley, Braithwaite *et al.* 1973; Heinrich 1989). The primary role of the female in constructing the nest lining is reported to be the case in many corvids species, although Goodwin (1977) suggests that in some cases this is not confirmed but only assumed by observers that the bird doing most of the work on the lining is the female. Heinrich (1988) found that in some Common Raven pairs he studied the male did

most of the lining, while in other pairs both members contributed equally; similarly, is more often the male Rook which constructs the lining (Goodwin 1977). It was possible in the current study that the nest lining was constructed by both males and females, but only one at a time.

Nest construction was accompanied by soft crooning calls by both the male and the female. While these sounds were made even when a raven was alone at the nest, they sounded the same as the soft contact calls made during pair-bonding behaviour such as allopreening. This suggests that nest building may be a form of bonding, a theory which is supported by the known role of photoperiod and sex hormones in nest construction behaviour in some birds (McDonald 1982; Mota and Depraz 2004; Hill *et al.* 2005). Nest-building and coitus may be closely associated in birds, often occurring simultaneously (Bastock 1967).

The nest construction process observed in Forest Ravens was consistent with that of other corvid species (Rowley 1973c; Hansell 2000). Sticks were often collected from some distance from the nest and appeared to be carefully selected. Sticks were rarely taken from the ground, but instead were broken off trees. Some sticks were dropped immediately, suggesting that they were deemed unsuitable for the nest. The nest lining, and occasionally the wall, often incorporated man-made materials as well as natural materials such as mud, manure and shredded bark. The composition of the lining of the nest was determined by the characteristics of the area in which the nest was located: nests in or around farmland areas commonly included baling twine and horse manure in their lining. Some nests also contained shredded plastic from shopping bags or packaging. The use of bark as a lining material is common in a wide range of corvid species while, as here, other materials depend on the location of the individual nest (Butler *et al.* 1984).

Nest re-use

Forest Raven nests were sometimes used for more than one breeding season. While Northern Ravens have been known to nest in the same site for at least six

years (Stiehl 1985), Forest Raven nest sites were not used for more than two nesting seasons consecutively; this observation may be due to the short duration of the current study. In a single territory (PM01) the 2005 nest site was re-used in 2007, after nesting occurred elsewhere in 2006. This raises the distinction of the re-use of nest sites as opposed to the re-use of nests: when a nest site was used in two consecutive years the existing nest was refurbished in the second year, while in the case of the PM01 ravens a new nest was built, as the existing nest had been virtually demolished in the intervening time.

Nest re-use is a trade-off between a number of factors (Hansell 2000). The reasons for building a new nest or re-using an existing nest are unclear in corvids, even from long-term (up to 50-year) studies of Northern Ravens in Britain, which exhibit no apparent pattern in their annual movements between nest sites (Ratcliffe 1997). The re-use of nests may have significant benefits through a reduction in the energy and time cost of building, although repairing an old nest still takes time and energy for the collection of sticks and re-building (Hansell 2000). Earlier clutches tend to be more successful in many bird species including the American Crow (Ignatiuk and Clark 1991). In this study, the timing of nest construction was similar to the timing of refurbishment of existing nests. Although this was not tested statistically, it is likely that any variation in timing between these activities would have been so small as to not be biologically relevant. This suggests that for Forest Ravens in this study there was no benefit to refurbishing a nest in terms of the ability to lay earlier and therefore no associated increase in nest productivity. There was no apparent correlation between the number of fledglings produced and the history of the current nest, although Rowley (1973) reported that a lower proportion of re-used nests produced fledglings than newly-built nests in the Australian Raven. This may have been a result of the relatively small sample sizes used in this study, or may indicate that Forest Ravens were very good at determining whether a nest is in appropriate condition for re-use. Again, this suggests that the energy saved by refurbishing a nest over building a new nest was minimal relative to that required to produce a successful brood of young. The data used in this study included the total

productivity of each pair for each year; where the first nesting attempt was unsuccessful, the productivity of the second nesting attempt was used. There was a slight, but non-significant reduction in productivity of second clutches; this, added to the fact that new nests are built for second clutches, may have produced a slightly lower mean productivity for new nests than would be otherwise expected.

The productivity of a nest did not appear to influence whether it was re-used in the next year, although in other corvid species nest sites characterised by low reproductive success are less likely to be reused (Tryjanowsky *et al.* 2004). Such a relationship may work in opposite directions: low productivity may be in part attributed to poor nest site in terms of conspicuousness and predation risk (Cresswell 1997), while conversely a large brood would be expected to foul the nest considerably more than smaller brood, and thus make the nest more conspicuous while also increasing parasite loads. Parasites are a negative consequence of re-using nests (Hansell 2000), but this may have been mitigated in Forest Raven nests by the discarding and replacement of old lining materials seen on some occasions; this has also been reported in Australian Ravens (Rowley 1973c). Large numbers of unidentified invertebrates and seeds in discarded nest lining found beneath nests may have entered while the lining was in place, in which case nests collected considerable loads of waste and insects during the nestling, and possibly the egg, phases of nesting. Removal of faecal sacs by parents helps to keep nests free from insect infestation when nestlings are young (Weatherhead 1984), but Australian Raven nestlings fouled the outside of the nest when they were large enough to defecate over the edge (Rowley 1973c). Ratcliffe (1997) reports that some studies of Northern Ravens have found no correlation between success and failure, and the re-use or otherwise of nests, while other studies have found a strong correlation between these factors. Ratcliffe does not, however, mention whether the number of offspring from a successful nest influences nest re-use.

In a single case, Forest Ravens nested in an old nest site from which they had been absent for a nesting season. These ravens, from the SL01 territory, almost completely demolished and re-built their second nest from 2005, to use as their first nest in 2007. This has been reported in Northern Ravens, which are known to have a selection of nest sites to which they return apparently at random (Ratcliffe 1997). Conversely, Rowley (1973c) does not record Australian Ravens returning to nest sites after absences, but does report that an old nest may be refurbished if an urgent re-laying attempt is being made after failure of a clutch. In contrast to many other corvid species (Holyoake 1967; Ratcliffe 1997), Forest Ravens were not seen to re-use first nests for replacement clutches; a new nest was always built, with the possible exception of one clutch which may have been lost very soon after laying. This result may be due to the relatively short duration and small sample sizes of this study: long-term observations of individual raven pairs may show that in some cases nests are re-used in the current nesting season. New nests built for replacement clutches tended to be located relatively close to the first nest of the season. While appropriate trees were always available for this purpose during this study, further study into the importance of a second appropriate nest tree in original nest-site selection and the ability to re-lay would be of interest for land management in areas of increasing urbanisation.

In many cases two nests were built close together at the beginning of the nesting season, only one of which was used. The other nest may have acted in part as a decoy nest: Secomb (2005b) reported apparent decoy behaviour in Northern Forest Ravens during nest construction, with a raven taking a stick to an old nest nearby when an observer approached. It is possible that the nests seen in this study also acted as decoys during the nesting period. Northern Forest Ravens used stick structures as food cache sites (Secomb, 2005a), but in the current study Forest Ravens were not seen to approach these nests to collect food. After fledging, however, the "spare" nest may have been used as a "dormitory" for fledglings, and possibly at least one adult, before the young birds were able to fly far from the nest area. Where a second nest was not built, previously-used nests may have been used for this purpose. While the use of dormitory nests by birds

has been thoroughly studied (Skutch 1961), it does not appear to have been reported in the corvids. Juvenile Common Ravens often returned to the immediate vicinity of the nest at night (Ratcliffe 1997), and young Australian Ravens returned to the nest to roost at night for the first four to five days after fledging (Higgins *et al.* 2006), but neither species has been reported using a purpose-built nest as a roost. In Forest Ravens, this "spare" nest was never used for breeding; even in the event of the failure of a first clutch, a new nest was built. This may indicate that these nests were unsuitable for breeding, or may have reflected the importance of roost nests for some pairs.

During incubation, it was assumed that the female spends the night on the nest. Evidence suggested that the male often roosted in an old nest, which may be some distance from the active nest. This is generally consistent with Ratcliffe's finding that male Common Ravens usually had a favoured roosting place within 100m of the nest during incubation (Ratcliffe 1997). This is also seen in the Brown Cachalote (*Pseudoseisura lophotes*), a species in which juveniles initially roost in their nest then move to a dormitory nest built and used by the parents after the young are reared (Nores and Nores 1994).

2.4.2 Nest success and productivity

Forest Ravens from the six territories in this study produced a total of 36 fledglings over 19 pair-seasons, giving an average of 1.89 fledglings per pair-season, ranging from zero to three young per nest.

Through their effects on clutch size, egg hatchability and nestling survival, a wide range of environmental and intrinsic factors have been recognised as affecting the success and productivity of nesting attempts in birds. Many of these are related to food availability: the ability to provision nestlings is a primary limiting factor in the number of fledglings ultimately produced in a nesting attempt. Experimental provision of extra food led to earlier laying and increased nest productivity in Northern Ravens (Yom-Tov 1974) and Jackdaws (Soler and Soler 1996), while

drought reduced the proportion of successful nests in one study population of Australian Ravens (Rowley 1973c). The effect of habitat on breeding success was reported by Marquiss *et al.* (1978), who found an increase in non-breeding and the production of later, smaller broods in Common Raven pairs residing in afforested areas: Common Ravens preferentially forage in more open areas (Ratcliffe 1997), suggesting food supplies in heavily forested areas were lower. McGowan (2001) suggests that greater food availability and reliability was the reason for the significantly higher productivity of rural than suburban American Crow nests in New York. As well as preventing nestling starvation, large quantities of food in the nest area reduce the time adult birds must spend away from the nest, and therefore the risk of predation (Yom-Tov 1974). In the current study, neighbouring pairs holding territories within the same habitat, often exhibited quite different nest productivities. Consequently it can be assumed that habitat, if it influenced nest productivity, was not the primary factor influencing productivity in the ravens studied here. In this study, provisioning rate and nest attentiveness throughout the nesting period did not appear to be related to the number of fledglings produced.

The use of data from a number of pairs or territories over multiple years for determining average nest productivity reduces the chance of inaccuracies arising from the inadvertent selection of an anomalous year, and is common in studies of breeding biology of bird populations (e.g. Butler *et al.* 1984). However the relatively small number of territories included in the current study may be insufficient to reduce the influence of inter-pair variation on the results, as repeated measurements from one territory, while reducing possible biasing of data from an atypical year, will still produce a biased result if that territory is atypical. While considerable variation was seen in average nest productivity between the territories with highest and lowest productivities, removing these from the data did not greatly affect the results (2.00 as opposed to 1.89 young/pair/season). Within the limitations of the data, the results of the current study are comparable to the 1.8 fledglings (1-3) per pair-season (n = 6) for Northern Forest Ravens cited

by Secomb (2005b). Australian Ravens at Geary's Gap, southern New South Wales, reared on average 1.53 young per pair (Rowley 1973c).

The timing of breeding in many bird species is influenced by day-length, and therefore the time available for foraging, during the nestling phase (McDougal-Shackleton and Hahn 2007) In addition, the timing of breeding in many species is related to the peak availability of a specific food source, and it is possible that later-hatching broods may miss this period. A relationship between nest productivity and the timing of nesting has been recognised in corvid species (Yom-Tov 1974; Ignatiuk and Clark 1991). The sample sizes in the current study were too small to detect any relationship between Forest Raven nest productivity and time throughout the breeding season. The clutches producing three nestlings were laid relatively early in the season, however early clutches also produced zero, one or two fledglings indicating that other factors were involved in determining nest productivity in Forest Ravens.

Overall, among all years and territories the most common brood size of the ravens in this study was two. This was also the case for three individual territories (LW01, PM02, UT01), however the mode for each of the remaining territories varied from zero (SL02) to three (SL01). Some ravens in this study, such as those from the LW01 and SL01 territories, were consistently successful breeders, producing average or above-average broods in each nesting season. Others, such as the SL02 ravens, produced fewer than average fledglings in all nesting seasons. In five of the six focal pairs annual productivity varied by no more than a single fledgling across three nesting seasons. In contrast, the PM01 ravens produced one, zero and three fledglings in the 2005, 2006 and 2007 breeding seasons respectively. A similar situation occurred in the Australian Raven (Rowley 1973c) and the American Crow (Caffrey 2000), in which some pairs consistently produced large broods. The current study was too small to attempt to identify reasons for this, however studies of other corvid and non-corvid bird species have suggested that nest productivity is influenced by the age and experience of the

parent birds (Ignatiuk and Clark 1991; Robertson and Rendell 2001), while clutch size may be inherited (Yom-Tov 1974).

Average nest productivity of the six focal raven territories was consistent within a small range across the four nesting seasons included in the current study. The lowest mean productivity was observed in 2006, when the ravens produced on average 1.5 fledglings per territory. The highest mean productivity, 2.2 fledglings per territory, was seen in 2007. Within the study area, none of the nesting seasons included in this study were abnormally wet or dry. It may be assumed that in such aberrant nesting seasons annual mean productivities would lie outside the range found in the current study.

Juvenile survival

The period between leaving the nest and becoming independent of parental care is a time in which young birds learn vital life-skills and face high risk of mortality (Wheelwright *et al.* 2003). Despite this, of the 36 juveniles to fledge during this study, all but one survived their first month out of the nest. The one juvenile death occurred very soon after fledging; the bird died three days after being found tangled in a vine beneath the nest tree, possibly after failing its first flight. A similarly low juvenile mortality rate was seen in Australian Ravens (Rowley 1973c). Conversely, only 56% of fledged young in a population of American Crows survived their first two weeks out of the nest (Caffrey 1992), and in a desert population of Northern Ravens only 38% of young survived to leave the natal territory (Webb *et al.* 2004).

Commonly cited causes of juvenile mortality in crows and ravens include predation, human persecution, starvation, disease, becoming tangled in vegetation, and injury from anthropogenic sources such as cars and powerlines (Chamberlain-Auger *et al.* 1990; Caffrey 1992; Ratcliffe 1997; McGowan 2001; Webb *et al.* 2004). In California, juvenile Northern Ravens from nests relatively close to human resources were increasingly likely to be killed by anthropogenic sources

rather than natural sources (Webb *et al.* 2004). The current study was undertaken in light, semi-suburban bushland; in such habitats cars and powerlines, predation, and entanglement are most likely primary causes of juvenile raven mortality. In agricultural areas, it is likely human persecution is a cause of juvenile mortality: in Tasmania, Forest Ravens are not protected by law and are commonly shot or poisoned by farmers for their perceived role in lamb and sheep deaths (Jones and Park 2005).

While the one-month survival rate of juvenile ravens is of interest as a starting point for longer-term survival, more extended research is required for determination of recruitment rates to flocks and adult populations. This is, however, difficult: older juveniles of many bird species are increasingly difficult to follow and observe (Rowley 1973c; Wheelwright *et al.* 2003) as they fly farther from the nest area. This was made even more difficult in this study by my inability to band and subsequently recognise individual birds. It is possible that older juveniles may be easier to capture than the newly-fledged young which were targeted in the current study, as parental supervision and warning of potential threats declined with juvenile age. If so, future studies in which banded juveniles are followed, added to findings of this study, may provide useful information on recruitment rates of Forest Ravens in Tasmania.

2.4.3 Breeding season

Forest Ravens in this study nested between late winter and mid-summer. Laying began in early-mid August, and the latest fledgling left the nest on January 11th. First clutches generally fledged in November.

As the Nest Record Scheme holds few specific records of Forest Raven breeding (Higgins *et al.* 2006), and the sample sizes used in the current study were small, accurate comparisons of breeding season among populations and species was not possible. Despite this, Higgins *et al.* (2006) suggest that the breeding season of Forest Ravens in Tasmania is "apparently" later than on mainland Australia.

Forest Raven eggs have been reported between July and September in New South Wales, and nestlings between September and October in New South Wales and Victoria; in Tasmania, eggs have been recorded between late September and mid-December (Higgins *et al.* 2006). Figure 2.27 shows that eggs were present earlier in this study than hitherto reported for Tasmania; the existing data are obviously incomplete given that the earliest dates in which eggs and nestlings have been recorded are the same. The results of this study reduce the perceived differences between Tasmanian and mainland Forest Raven breeding seasons: nestlings were recorded both in Victorian nests, and those in this study, from early September.

Food availability is an important factor in the timing of birds' breeding seasons, both within and between bird species (Follet 1984; Wyndham 1986; Cockrem 1995). Ultimately, the breeding season of Rooks was regulated to ensure hatching occurred at the time of peak earthworm levels, although the proximate regulator was changing photoperiod (Follet 1984). The timing of fledging in Australian Ravens was apparently influenced by the development of local grasshopper swarms (Rowley 1973c). This may have been due to the increased availability of grasshoppers as a food source for the fledglings, or may be related to the influx of nomadic flocks into the area, which the juveniles would eventually join. There was no evidence in the current study that the availability of a specific food source was a factor in the determination of Forest Raven breeding seasons. Despite this, Rowley's (1973c) argument that winter-spring breeding seasons are optimum for breeding in temperate-climate omnivorous corvids due to winter rainfall, the consequential flourishing of insects and small animals in spring and the fact that carrion lasts longer in cooler weather (Rowley 1973c) is most likely applicable to Forest Ravens in Tasmania.

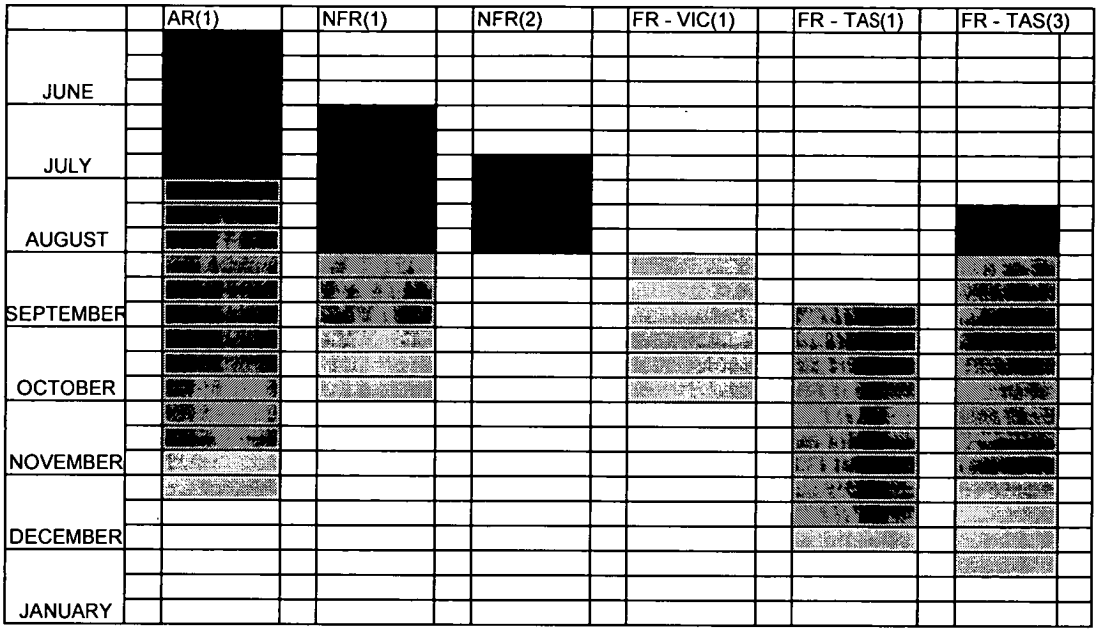


Figure 2.27 Presence of eggs and nestlings in nests of Australian Ravens (AR), Northern Forest Ravens (NFR), Forest Ravens in Victoria (FR-Vic) and Forest Ravens in Tasmania (FR-Tas). Black, egg records; grey, nestling records; cross-hatched, overlap of egg and nestling records. Sources: 1, Higgins *et al.* 2006 (number of records not reported); 2, Secomb 2006 (*n* = 5); 3, this study (*n* = 19).

Individual Forest Raven pairs were consistent in the timing of nesting, despite annual variation in rainfall and therefore, potentially, food availability. The small sample sizes of this study, both in the number of pairs and the number of nesting seasons covered, were insufficient for the determination of weather-related patterns in breeding success or timing, as many other factors would be involved which may obscure such trends.

Ravens from two territories were successful in their first nesting attempts for each of the nesting seasons in which they were observed; in each of these territories incubation began within a five-day period across three or four years' observation. Other ravens exhibited a wider spread of incubation dates. This may have been a

result of less success in first attempts, but in a number of late nestings the failure of a first clutch had not been confirmed.

Length of nesting phases

The time between the onset of incubation and hatching in Forest Ravens in this study was consistently estimated at 22 to 23 days. This gives a slightly longer incubation period for the species than that of the Australian Raven (19-21 days) reported by Rowley (1973c) and from collated nest records (Higgins *et al.* 2006), and the 20 days assumed by Secomb (2005b) for Northern Forest Ravens, as well as the usual incubation periods of most other corvid species (Holyoake 1967; Madge and Burn 1994). As incubation periods vary within species it is unknown whether the results of this study reflect a significant difference in incubation period between Forest Ravens and other corvids.

Most corvids lay eggs at intervals of one or more days (Goodwin 1977). In such cases incubation often starts before the clutch is complete (Holyoake 1967; Wilmore 1977). Australian Ravens incubate from the laying of the first egg, but incubation is irregular until the third or fourth egg is laid (Higgins *et al.* 2006). The time at which incubation starts varies among species (Holyoake 1967). The uncertainty of when incubation begins makes the length of the incubation period difficult to calculate (Holyoake 1967), particularly when little is known of the laying and hatching behaviour of the species, as in the Forest Raven. Differences in the onset of incubation relative to the laying of the first egg may in part explain differences in the incubation periods of Australian Ravens and Forest Ravens.

Possibly increasing the difficulty raised by differences in the onset of incubation is the fact that the eggs of most altricial bird species hatch asynchronously over one or more days (Slagsvold *et al.* 1992). In Australian Ravens the first two eggs in the clutch generally hatch together, with the third hatching later that day (Higgins *et al.* 2006). The time between laying and hatching therefore differs among eggs in a clutch; indeed, the incubation period of an individual egg is

dependent on the size of the clutch and the chronological position of that egg within the clutch (Rowley 1973c). This is assumed to be the case for most birds (Cook and Monaghan 2004), and is likely to be the case for Forest Ravens also. Because I was unable to see inside nests, and consequently unable to determine laying and hatching intervals, the exact length of the nesting phases of Forest Ravens could not be determined in this study, although estimates could be made based on parental behaviours such as incubation and the onset of feeding behaviour at the nest. The assumption was made that nestlings were fed from the first day after hatching.

The rate of embryonic development in birds, and therefore the length of the incubation period, is associated with egg temperature (Strausberger 1998; Deeming *et al.* 2006), which is determined by a range of factors. Of these, one of the most often cited is egg mass: the length of incubation periods in many bird species is positively correlated with the weight of the egg (Rahn and Ar 1974; Drent 1975), although the nature of the variation varies between avian orders (Deeming *et al.* 2006) and is not universal, for example in Black Brant (Eichholz and Sedinger 1998) and Black Guillemot, (Cook and Monaghan 2004). Furthermore, egg dimensions may vary widely within species (Zduniak and Antczac 2003). The dimensions of Australian Raven and Forest Raven eggs are similar (mean = 45 x 30.3cm and 44.9 x 31.1 cm respectively; Higgins *et al.* 2006), suggesting that this is not the primary factor involved in the discrepancy between the incubation periods of the species.

External factors are also known to affect egg temperature. These include the insulation properties of the nest and the prevailing ambient temperature (Deeming 1998), although these do not necessarily affect incubation period length (Eichholz and Sedinger 1998). No data are available on geographic variation in incubation periods for either species or the insulation properties of the nests, but these may be important as cooler incubation environments can lead to slower embryonic development among conspecifics (Drent 1975; Martin *et al.* 2007). Reduced nest attentiveness, and the associated lowering of egg temperatures, may increase

embryonic development times (Chalfoun and Martin 2007). Forest Ravens in this study exhibited slightly lower nest attentiveness than other corvid species for which data were available ((Butler *et al.* 1984; Ratcliffe 1997; Secomb 2005b), although the relationship between nest attentiveness and incubation period length would involve many other factors and could not be tested here.

Nest attentiveness has been found to influence egg temperature (Tieleman *et al.* 2004; Martin *et al.* 2007) and periodic cooling of the eggs may delay embryonic development and reduce the efficiency with which nutrients are converted to embryonic tissue (Olson *et al.* 2006). While some authors have found a correlation between nest attentiveness and incubation period (Martin *et al.* 2007), others have found that the two factors are not related (Eichholz and Sedinger 1998; Olson *et al.* 2006). It has been shown in this study that the attentiveness of incubating Forest Ravens varies considerably among pairs and to a lesser extent, nesting seasons; given this, further study into the effects of this on incubation period would be of interest.

Assuming an average of 22 days incubation (from the start of incubation), the duration between hatching and the time at which the first fledgling leaves the nest ranged from around 37 to 49 days. As with incubation period, this is longer than in other corvid species including the American Crow, Northwestern Crow, Rook and Hooded Crow (Ignatiuk and Clark 1991), but is consistent with the Australian Raven in which the period between hatching and fledging ranged from 40 to 45 days (Rowley 1973c). Variation in the length of this period was not related to territory or nesting season, suggesting that habitat, weather or genetics were not primary influencing factors. Due to the small size of the current study, an investigation of the relationship between fledging period and brood size could only be undertaken by grouping all years and territories, however it was assumed that given the apparent lack of correlation between fledging period and territory or year any inaccuracies which may have arisen as a result of pseudoreplication would be at most minimal. Given this, as in American Crows (Ignatiuk and Clark

1991) the length of the nestling period in Forest Ravens did not appear to related to the number of fledglings produced as it is in the Jackdaw (Soler 1988).

In the current study the time between hatching and fledging was estimated for the fledgling which left the nest first, as young Forest Raven brood-mates fledged asynchronously. The difference in fledging date of brood-mates was dependent on the size of the brood: while in broods of two the young fledged within three days of each other, up to six days' difference in fledging date was seen between the first and subsequent young in broods of three. Asynchronous hatching may lead to disparity in the development of brood-mates, with last-hatched nestlings having slower growth and reduced survival (Krebs 1999). Asynchronous hatching in Australian Ravens allows for flexibility in the number of young raised by facilitating brood reduction in poor nesting seasons, while in good years all nestlings can be fed and survive to fledge (Rowley 1973c). In such cases the growth of the latest-hatched nestling may catch up with that of its brood-mates, and it can fledge a normal-sized, strong bird; alternatively, the youngest may fledge at a smaller size than its siblings (Rowley 1973c). For Forest Ravens, slower development of younger nestlings in larger broods may explain the large discrepancy in fledging dates among siblings in a three-bird brood; however, while the first bird may fledge several days before the third, the second and third young fledge together, suggesting that differing rates of development alone cannot explain fledging intervals in Forest Raven broods, although the 3-4 day spread of fledging dates in large broods of Northern Ravens has been attributed to this (Ratcliffe 1997). Older Australian Raven nestlings are sometimes reluctant to fledge before smaller siblings because the nest is the focus of parental attention as long as it is occupied (Rowley 1973c); this may in some way explain the variation in the spread of within-brood fledging dates among broods.

2.4.4 Parental care

Parental care in birds may include incubation of eggs, brooding and provisioning of nestlings, and protection of eggs and nestlings from predation. Extended

parental care is common in corvids, with juveniles of most species remaining dependent on their parents for at least several weeks after fledging (Marzluff and Angell 2005). While parental care increases survival of young, it may be costly for parents in terms of energy, time and survivorship (Henderson and Hart 1993; Woodard and Murphy 1999; Wheelwright *et al.* 2003). Here, incubation and provisioning behaviour were investigated in three Forest Raven territories in southern Tasmania.

Parental roles

In many socially monogamous bird species which produce altricial nestlings, the male plays a significant role in care of the young (Stenhouse *et al.* 2004), although the extent of male parental care varies widely among species (Ligon 1999). In the Forest Raven both parents were involved in care of the young throughout the nesting and juvenile phases. In this study it was not possible to determine which member of a breeding pair was on the nest at any time; in the majority of corvid species (Goodwin 1977; Madge and Burn 1994), including the Australian Raven (Rowley 1973c), only the female is known to incubate. Occasional observations of crossovers, in which a brooding adult Forest Raven left the nest and was replaced on the nest by its mate, indicate that both parents are involved to some extent in brooding behaviour. In the Northern Raven the female undertakes the majority of brooding behaviour, although she may be relieved by the male in order to exercise and forage; in such cases, she usually returns to the nest within the hour (Ratcliffe 1997). Rowley (1973c) did not record Australian Raven males brooding nestlings. It is said that Northern Raven males do not brood properly, but stand or crouch over the nest (Ratcliffe 1997). In one observed case in this study when a brooding Forest Raven left the nest the mate did stand over the nest; in other cases, the "replacement" adult appeared to be sitting on the nest, but may instead have been crouching low over the nestlings. The extent of brooding activity by male Forest Ravens could only be determined in future studies if individuals can be caught, sexed and banded.

Nest attentiveness

Ambient temperature is an important factor in the rate and success of embryonic development (Deeming *et al.* 2006). In birds, nest attentiveness - that is, the temporal pattern in which a bird is on the nest – may influence the ambient temperature within the nest (Tieleman *et al.* 2004; Martin *et al.* 2007). In altricial bird species, in which young hatch naked and unable to maintain body heat, brooding allows control of the nest environment and reduces predation risk, and therefore facilitates nestling survival.

During incubation, Forest Raven nests were covered for 82% of observations across all nests and years; this is contrary to the assertion of Cooper *et al.* (2005) that most Passerine species exhibit nest attentiveness levels below 75%. The overall time spent on the nest by Forest Ravens in this study equated to around 49 minutes in every hour, comparable to 52 minutes per hour in Northwestern Crows (Butler *et al.* 1984) and 53 and 59 minutes per hour in Northern Forest Ravens (1996 and 1997 respectively; Secomb 2005b). In one study, a Northern Raven nest was unattended for around 11% of the daylight period (Ratcliffe 1997), equating to around 53 minutes per hour in which the nest was attended.

Overall, the ravens from each territory were consistent in the level of nest attentiveness they exhibited across the three nesting seasons. The exception to this was the UT01 ravens, in which nest attentiveness was significantly lower in 2006 than in other years. The nesting attempt observed in this territory in 2006 occurred considerably later (November-January) than in 2005 or 2007 (September-November), and was also the latest observed nesting attempt seen in this study. Mean temperatures (mean daily maximum, mean 0900h temperature and mean 1500h temperature) were generally higher between November 2006 and January 2007 than between September and November 2006 (Australian Bureau of Meteorology). Australian Ravens increased brooding constancy in bad weather (Rowley 1973c), and the amount of time Forest Ravens spent on the nest increased during rain or temperature extremes (this study); even when feathered, nestlings are vulnerable to weather conditions and brooding affords protection

against rain, cold temperatures or strong sun. Accordingly, the lower nest attentiveness seen in the UT01 territory in 2006 may have been a result of warmer ambient temperatures.

Alternatively, the lateness of this nesting attempt suggests that this was a second clutch. This may explain reduced nest attentiveness, given that parental resources would be reduced from the first nesting attempt; however, reduced nest attentiveness was not observed in the 2005 PM01 nesting attempt which, beginning in October, was later than the September onset of the failed 2006 and successful 2007 nesting attempts. The lack of variation in nest attentiveness, and the relatively small difference in the timing of nesting attempts across nesting seasons in the PM01 ravens, supports the theory of reduced nest attentiveness in more clement conditions for the UT01 case.

Nest attentiveness decreased steadily as the nestlings aged. When the anomalous UT01 2006 nesting attempt was excluded, ravens from all three territories exhibited parallel decreases in nest attentiveness throughout the nestling period, although the ravens differed significantly in the overall amount of time they spent on the nest. The UT01 ravens were the most attentive, while the SL01 ravens spent the least time on the nest. This reflected differences in the frequency of visits to the nest: the UT01 ravens visited the nest more often throughout the nestling phase than the SL01 ravens. In the Northern Raven, the total frequency of feeding increased with brood size (Thoni 1997), while a positive correlation was found between male provisioning rate and the number of chicks fledged in the Jackdaw (Henderson and Hart 1993). As nest productivity varied within pairs, and the number of young nestlings could not be determined, it was not possible in the current study to test the relationship between visiting rate and Forest Raven brood sizes.

In the Northern Raven, *Corvus corax*, pairs with more than one nestling save effort by stopping brooding at an earlier stage than in broods of one (Thoni 1997). Only one nesting attempt in this study (PM01 2005) produced a single fledgling,

but brooding did not clearly cease sooner in this nesting attempt than in others. A test of relationship between brood size and brooding period would require knowledge of the number of hatchlings in a brood, which was not possible in this study.

While on the nest, an incubating or brooding raven was at times fed on the nest by its mate. The frequency with which this occurred varied from zero to five times per hour. Incubation feeding is common in the corvids (Goodwin 1977), along with some other Passerine birds (Lyon and Montgomerie 1987). By reducing the need for the incubating bird to leave the nest to feed, incubation feeding may reduce nest predation risk and reduce the amount of time in which the eggs are uncovered and therefore the potential for cooling. Although a bird on the nest expends less energy than a bird perched outside a nest, long periods spent incubating, with the associated decrease in the amount of time available for foraging, increase the required amount of energy acquired in each foraging bout (Walsberg and King 1978b). This conflict between time spent incubating and time spent foraging may be mitigated by incubation feeding.

Although there was an overall decrease in nest attentiveness and nest visit frequency with increased nestling age, considerable daily fluctuation could be seen for all pair-seasons. In many cases these outliers could be explained by climatic or other external factors. Local flock activity, or the presence of other potential predators, often resulted in slightly lower than expected nest attentiveness or visit frequency. In the Australian Raven brooding constancy may increase in bad weather despite a general decrease in brooding constancy over time (Rowley 1973c), as even when feathered, nestlings are vulnerable to weather conditions and brooding affords protection against rain, cold temperatures or strong sun. Although no quantitative data on weather conditions were collected in the course of this study, it is likely that Forest Raven nest attendance and visit rate may have also been influenced by prevailing weather conditions.

Provisioning

The ability of parents to provide food is a limiting factor in the productivity of a nest, and imposes considerable time and energy costs on the parents (Henderson and Hart 1993). Starvation has been identified as a major cause of nestling deaths in corvids such as the Jackdaw (Henderson and Hart 1993), the Northwestern Crow (Richardson *et al.* 1985) and the American Crow (Ignatiuk and Clark 1991), while provisioning rate by males was found to be significantly correlated with nestling growth rate and nest productivity in Jackdaws (Henderson and Hart 1993) and experimental increases in food availability increased nestling survival in Carrion Crows (Yom-Tov 1974). A shortage of food in the nest area not only leads to the risk of chick starvation, but also may increase the time parents must spend away from the nest and therefore the risk of nest predation (Yom-Tov 1974). Predation risk may also be increased through the greater detectibility of hungry, noisy nestlings (Slagsvold 1982). In the current study an incubating bird was led to a food cache near the nest by its mate; cached food was also fed to juveniles. This suggests that Forest Ravens reduce the costs and risks of provisioning through the storage of food before nesting, or when food supplies are readily available. The use of cached food for provisioning nestlings has also been observed in Torresian Crows (Secomb, 2005c) and Northern Forest Ravens (Secomb 2005a).

In the current study the frequency and decrease in nest visits, and therefore feeding of nestlings, was consistent across the three nesting seasons in each of the SL01 and UT01 territories. In contrast, the 2005 and 2007 nesting attempts of the PM01 ravens varied significantly in both the overall frequency of visits to the nest throughout the nestling phase, and the extent of the decrease as the nestlings aged. In 2005, the PM01 parents visited the nest more frequently in the early nestling stages than in 2007, but the frequency of nest visits declined more rapidly in 2005, ending at a lower frequency at the time of fledging than in 2007. Again, this may be due to the observed 2005 nesting attempt being a second clutch, but this alteration in nest visit frequency was not observed in the other observed second nesting attempt, that of the UT01 pair in 2006. More likely, significant, prolonged

flock activity around the PM01 territory in 2005 may have affected parental behaviour by initially increasing the frequency with which the brooding bird left (and subsequently returned to) the nest and by later reducing the opportunity to visit the nest: nesting ravens in all territories were observed to spend considerable time chasing intruding flock ravens from the nest area.

The decrease in nest visit frequency with time, seen in all pair-seasons of this study, is consistent with the pattern recorded in the Northern Raven (Ratcliffe 1997); it is, however, contrary to that of Australian Ravens in which feeding of young nestlings is infrequent, but increases as nestlings grow, until remaining steady at around four feeds per hour by 14 days post-hatching (Rowley 1973c). One study of Northern Raven breeding found that although parental attentiveness, in the form of visits to the nest, decreased as nestlings aged, the number of feeding visits remained relatively constant (Ratcliffe 1997). Feeding behaviour was seen in virtually all visits to nestlings in this study. In this study it was, however, impossible to determine how much food was provided to young at each visit. For Australian Ravens the amount of food brought in each visit increased as the nestlings grew, and after brooding ceased the amount of food utilised by the brooding female decreased (Rowley, 1973c).

Despite a clear ability to forage for themselves, young Forest Ravens continued to be fed by their parents up to two months after fledging. In other studies, provisioning of juveniles occurred for 77 days (Northwestern Crows; Butler *et al.* 1984) and for at least six weeks (Northern Ravens; Stiehl 1985). Rowley (1973c) reported that juvenile Australian Ravens are largely self-supporting by their third month (Rowley 1973c).

Local food availability has been found in many cases to influence reproductive success in birds, including corvids (e.g. Yom-Tov 1974; McGowan 2001); however, due to the small scale of the current study no analysis of food availability in the focal territories could be made.

Nest sanitation

Adult ravens visiting the nest cleaned the inside and, later, the outside of the nest of faecal waste from nestlings. Although limited data could be obtained on this behaviour, it appeared that in the early nestling stages faecal sacs produced by nestlings were often consumed at the nest by the visiting adult, while in later nestling stages faecal sacs were more often taken from the nest and discarded.

Removal of faecal sacs from nests serves several purposes, including keeping the nest dry, clean and free from insects (Morton 1979; Weatherhead 1984). Due to the white colour of avian faecal sacs they may be conspicuous to nest predators. Consequently their removal may reduce the risk of nest predation (Morton 1979; Weatherhead 1984). This may also occur if faecal sacs are discarded close to the nest; faecal sacs taken from Forest Raven nests were taken to nearby trees and smeared on a branch, therefore possibly reducing their visibility while reducing the potential cost of flying long distances to dispose of the sacs (Weatherhead 1984).

The apparent pattern of early faecal sac consumption giving way to faecal sac smearing seen in the current study is consistent with findings from other avian species (McGowan 1995). Due to the immature alimentary tracts of young nestlings, early faecal sacs are highly nutritious and energy-rich, and therefore beneficial to adults if consumed (Morton 1979). Furthermore, faecal sacs may provide an important source of water to adults (Calder 1968). The nutritional benefit of consuming faecal sacs has been supported by findings in the American Crow, in which the more nutritionally stressed parent, the female, consumes more faecal sacs than the male (McGowan, 1995). In some species, as the digestive efficiency of nestlings increases, the nutritional and energy value of faecal sacs to parents decreases (Gluck 1988), although McGowan (1995) disputes this as a universal trend.

In Australian Ravens, towards the end of the nestling period nest sanitation by parents ceases and the outside of the nest becomes whitened as nestlings defecate

over the edge of the nest (Rowley 1973c). This also occurs in Forest Ravens, as well as other corvids including the Northern Raven (Ratcliffe 1997). Presumably at this stage the inside of the nest did not become fouled. Although one explanation for nest sanitation during the nestling period is the conspicuousness of excrement, Ratcliffe (1997) suggests that the smell of excreta from nestlings may deter predators from approaching the nest. In this study, however, when nestlings were sufficiently large to defecate on or over the nest rim, adult Forest Ravens continued to remove excreta from the outside of the nest; only in the last few days before fledging did the parents cease to clean the nest at all. It seems unlikely, then, that the cessation of nest cleaning is a means of nest protection.

2.4.5 Limitations of this study

This study was limited by a number of factors, two of which relate to the biology of the study species: the location of nests and the innate intelligence and caution of the species. The other main limitation of this study was the inability to collect many breeding data for Forest Ravens and the dearth of previous information on the species.

Most Forest Raven nests in Tasmania are located high in the top or outer branches of tall trees, between 18 and 40m above the ground. As a result, the nests can only be accessed by an experienced and well-equipped climber. Frequent employment of such a person was not viable for this study, for financial, time and safety reasons. Attempts were made to install cameras at raven nests, thus allowing the contents of the nest to be viewed from the ground at regular intervals. This was found to be highly problematic, as the cameras could be installed only at nests which could be safely accessed by an experienced climber, and which had appropriate branches nearby to which the camera could be attached. Cameras were eventually installed at three nests: one camera captured some images of nestlings before failing; a replacement camera moved in strong winds and no longer gave a view of the nest contents. In the other two cases the ravens abandoned the nest soon or immediately after installation of the camera. As a

result, the use of cameras was abandoned and clutch size, egg survival and hatchability and nestling survival could not be ascertained in this study. As collection of these data were initially primary aims of this study, the focus of the study had to be changed after the second nesting season; in some aspects of this study fewer than optimal results were collected due to the relatively short amount of time available for data collection in these areas.

Identification of individual Forest Ravens was also rendered impossible as no birds were captured and banded. Adult ravens are innately cautious of unfamiliar objects and appear to be particularly wary of traps; this has also been reported for other corvid species (Heinrich 1989; Ratcliffe 1997; Heinrich 1999; Marzluff and Angell 2005). Juveniles were less cautious, but were apparently warned away from the traps by their parents. A number of trap and bait types were used, including a trap design which has been used successfully on flocks of Australian Ravens (Rowley 1968). Traps were left in place (closed) for some time before they were baited, but all trapping attempts were unsuccessful. Forest Ravens are assumed to be similar to Australian Ravens in their long-term retention of territories and the development of pair-bonds which last until the death of one partner (Rowley 1973b); throughout the course of this study I did not find the carcass of an adult raven in any of the focal territories, although due to the extent of the territories such a thing could have been missed.

For a study of the breeding biology of a species to allow the clear identification of patterns in timing, productivity and adult behaviour, it must be undertaken over a long period of time. In the four breeding seasons available for this study a number of apparent trends have been discovered and questions raised: why, for example, did some pairs consistently have high nest productivity compared to some others, and is this a true difference or a short-term artefact of some unknown factor? Longer term studies of these, or other Forest Raven pairs, would provide answers to these questions.

The current study focussed on only six Forest Raven territories, all located in dry sclerophyll bushland in south-eastern Tasmania. This was necessary given the time scale of the study, the single researcher, and the inaccessibility of many raven nests. Rowley's (1973) study of - among other corvids - the Australian Raven was largely undertaken across extensive areas comprising relatively few individual properties (Rowley 1973a). In contrast, southern Tasmania largely comprises small properties relative to Forest Raven territory size; acquiring permission to access large numbers of private properties to locate and subsequently observe nests was not practicable in this case. Again, a larger-scale study would be beneficial to follow up the questions raised by the current study.

In some aspects of this study, the small sample sizes necessitated the grouping of data across territories or seasons without having tested the statistical independence of the data. It is possible that this may have led to inaccuracies in some cases, although given the nature of the data it was assumed that such inaccuracies would have been minimal particularly where the results presented were descriptive, such as overall productivity and timing. As few comparisons among territories or seasons were found to be statistically significant, it is unlikely that the results of this study led to false claims of correlation between tested factors.

2.5 Conclusion

This study investigated various aspects of the breeding biology of the Forest Raven in light forest habitats in southern Tasmania. Overall, within its limitations this study indicated that the breeding biology of the six focal Forest Raven pairs was consistent with that of other, ecologically similar corvid species, and consistent with previous assumptions concerning the breeding biology of Forest Ravens. The study raised a number of questions which would be of interest from an ecological, as well as a management, point of view if investigated in a larger-scale study undertaken over a longer time period and a wider geographical range.

3. ACTIVITY-TIME BUDGETS OF ADULT FOREST RAVENS IN TASMANIA

3.1 Introduction

Various activities, including feeding, anti-predator behaviour and personal maintenance, are vital for the day-to-day survival and reproduction of any animal (Verner 1965). The relative time spent in each of these activities depends on both the individual animal and the prevailing external conditions: a small, vulnerable animal surrounded by potential predators may need to spend more time in surveillance and predator-avoidance behaviour than a larger animal at the top of the food chain; similarly, a small active animal with a high metabolic rate may spend a relatively large amount of time feeding (Verner 1965). Any animal must balance the need to participate in particular behaviours with the energy cost or gain from such an activity.

Ambient temperature, season, time of day, habitat and day length have each been found to influence the activity patterns of birds, including corvids (Engel and Young 1992). The availability of food, and thus the efficiency of foraging, may vary seasonally or diurnally. This will often be reflected in the proportion of time a bird spends in feeding behaviour (Verner 1965) although this may be mitigated by a change in the type of food utilised (Moreno and Hillstroem 1992). Foraging leads to a net energy profit and consequently the activity budget of an animal should depend on the amount of time needed for the acquisition of the required amount of energy and nutrition (Lundberg 1985). Optimization of foraging techniques and locations reduces the time needed for foraging and increases the available time for other activities (Nahum and Kerr 2008).

Foraging and resting or surveillance behaviour are the most common behaviours in many bird species (Lundberg 1985; Sullivan 1990; Engel and Young 1992).

The time spent in these activities is likely to vary seasonally. Seasonal variation may also be expected in activities related to reproduction, including territoriality, courtship or bond-maintenance behaviours.

While activity and energy budgets have been undertaken on a large number of bird species, relatively few studies of corvid behaviour have been undertaken on territorial birds outside the breeding season. When Swinburne and Jessop (2005) studied the behaviour of Little Ravens *C. mellori* in Victoria, their study focussed on ravens in flocks or aggregations. The activity-budget study of Northern Ravens undertaken by Engel and Young (1992), and that by Saino (1994) on Carrion Crows, also focussed on individual corvids in flocks.

This study aims to develop an activity-time budget for resident adult Forest Ravens in Tasmania. Patterns in the proportion of time spent in various activities will be identified through comparisons among months and diurnal categories. The results of this study may be used in future studies of energy use in Forest Ravens. An understanding of Forest Raven behaviour may be of use in management of the species.

3.2 Methods

3.2.1 Study locations, times and subjects

The subjects of this study were adult, resident (territory-holding) Forest Ravens in Tasmania. Some individual ravens were observed more than once during the study, although no raven was observed more than once per month. The study sites were located around Tasmania, including small offshore islands (e.g. Bruny Island and Maria Island) and King Island in Bass Strait. The majority of observations were made in the south of the state. Focal ravens were generally located in accessible areas where they could be easily observed from a track, road or open area without the observer having to be too close to the bird.

The study was undertaken from 2005 to 2008 inclusive. Observations were made in all months and at various times of day to allow for seasonal and diurnal variation in behaviour patterns. Observations were classified based on time of day and season. For the former, four categories were defined:

1. Up to 0900h
2. 0900h-1300h
3. 1300h-1600h
4. 1600h onwards

All times are in Australian Eastern Standard Time (AEST) and disregard Daylight Saving. Where observation bouts crossed time-category boundaries the bout was included in data for the category in which the bout began.

3.2.2 Behaviour observations

Where necessary, observations of focal ravens were made using 9x21 Gerber binoculars. Due to the large size of Forest Ravens, behaviour of individuals could be easily determined at some distance, using either binoculars or the naked eye. Ravens which could not be clearly observed, due to distance or if sight was obscured by vegetation, were not included in this study. Behaviours used in this study were all easily recognised.

The behaviour and location of focal ravens was studied following the "Instantaneous Sampling" method described by Lehner (1996). A raven was observed continuously for as long as it was within sight. Observation bouts lasted between 2 and 23 minutes. During this time the behaviour and location of the focal raven was recorded at 30-second intervals. In many cases the raven moved out of sight; if it was out of sight for more than 1.5 minutes, the observation bout was stopped. If the raven came back into view in less than 1.5 minutes, and it was clearly the focal raven, the observation bout was continued and the missing records were excluded from the analysis. Observation bouts with fewer than four sampling points (individual observations) were excluded from the analysis.

At each sampling point, a record was made of the focal raven's behaviour and location, as well as whether the raven was interacting with any other bird.

Behaviours recognised were:

1. Vocalising
2. Surveillance
3. Preening
4. Flying, including long-distance flying and flights between trees. Short flights between branches of a single tree were classified as "moving"
5. Foraging

6. Moving: any short-distance movement, including short flights within a tree, hopping and walking. Walking was considered foraging behaviour if feeding behaviour occurred in the same observation bout
7. Courtship: this included any behaviour between members of a pair, such as allopreening and feeding
8. Aggression: actively chasing or exhibiting threatening behaviour towards other ravens or other species
9. Beak scraping or wiping
10. Other behaviour: this included behaviours which were rarely seen and did not fit under any other categories.

Locations recognised were:

1. In a tree
2. On the ground
3. In the air
4. On a stump or post, or any perch above the ground which is not a tree
5. Other locations

3.2.3 Analysis

The proportion of individual observations each focal raven spent in a particular activity was calculated as the number of individual observations of that activity divided by the total number of individual observations for that raven.

Proportional data were arcsine transformed before analysis (Engel and Young 1992). Analysis was undertaken on data from Autumn and Winter (March-August inclusive) only. Spring and Summer data were excluded from analysis as observations were only made away from the nest. Therefore these data did not include nesting activities and did not give accurate representation of the proportion of time spent in each activity. In all analyses individual observation bouts were used as sample units, the proportion of time spent in each activity as

dependent variables and Month and Time of Day as independent variables. Multivariate Analysis of Variance (MANOVA), in the SPSS 14.0 software package, was used to test for any time/month interaction.

If no interaction was present one-way ANOVAs were performed using the Statistica software package to identify differences between month or time of day in selected activities or foraging types, based on visual examination of graphed data. For all analyses $\alpha=0.05$.

3.3 Results

3.3.1 Non-breeding season activity-time budget

78 observation bouts, comprising a total of 1181 individual observations, or sampling points, were made of Forest Raven behaviour in Autumn and Winter (March-August) in the years 2004-2008. Surveillance was the most common activity, accounting for 44.9% of observations overall (Figure 3.1). Foraging accounted for 16.9% of observations overall, while vocalising was the third most prevalent activity accounting for 14.6% of observations (Figure 3.1).

Surveillance was the most common activity in all time categories (Figure 3.2a) and in all months except July (Figure 3.2b), when foraging accounted for the most observations. The large standard deviation bars in Figure 3.2 are indicative of the considerable variation in the behaviour of ravens among observation bouts, and may also be influenced by the varying length of observation bouts.

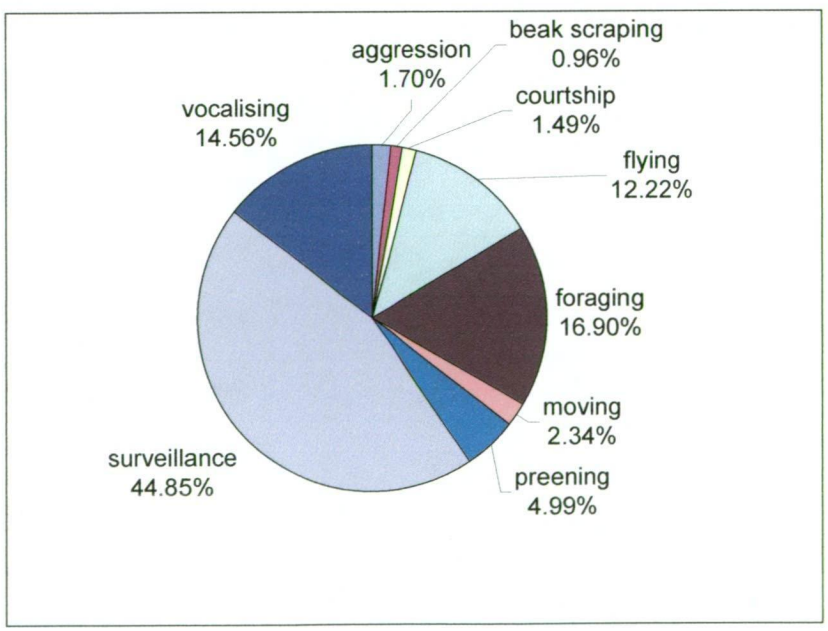
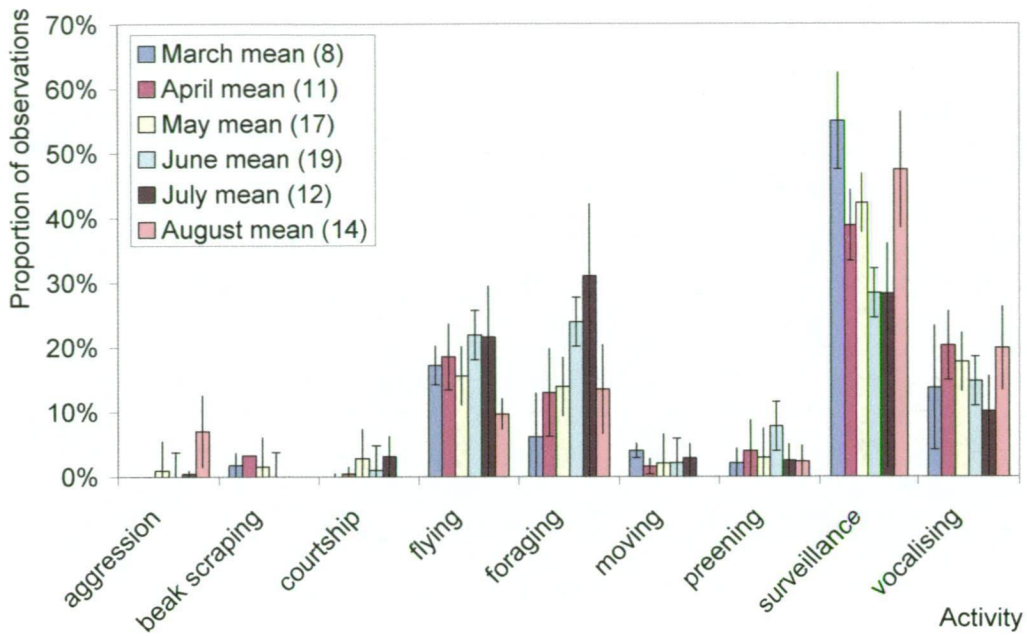
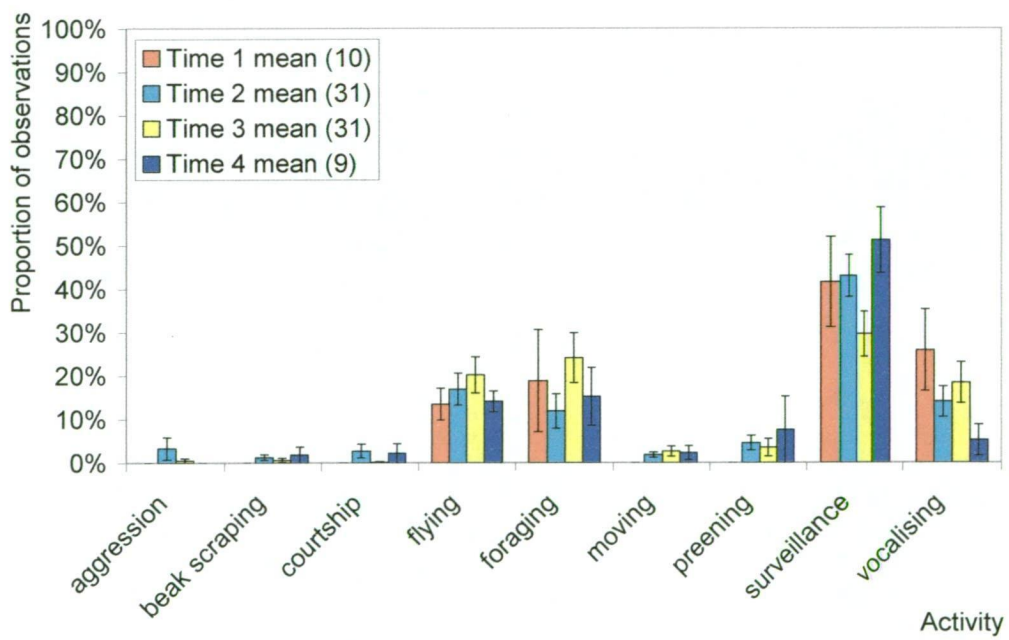


Figure 3.1 Proportion of time spent in various activities by Forest Ravens in Autumn and Winter



a



b

Figure 3.2 Mean (± SE) proportion of time Forest Ravens were observed in various activities by a, month and b, time of day

MANOVA found no significant variation in overall activity budgets among months (Pillai's V: $F_{40,275} = 0.91$; $P = 0.632$) or among diurnal periods (Pillai's V: $F_{24,159} = 0.84$; $P = 0.679$). Consequently, data from all months and from all diurnal categories were pooled for further analyses. Visual investigation of the proportion of time spent in each activity by month and by time of day suggested potential variation in foraging by month (Figure 3.3); and vocalising by time of day (Figure 3.4). When one way ANOVAs were performed on these data individually, no significant variation was found in any of these analyses, the results of which are given in Table 3.1.

Table 3.1 Results of one-way Analysis of Variance for the proportion of time Forest Ravens spent in selected activities, compared by month or time of day

Activity	*Independent variable*	*d.f.*	*F*	*P*
Foraging	Month	5	1.309	0.269
Vocalising	Time of Day	3	1.505	0.220

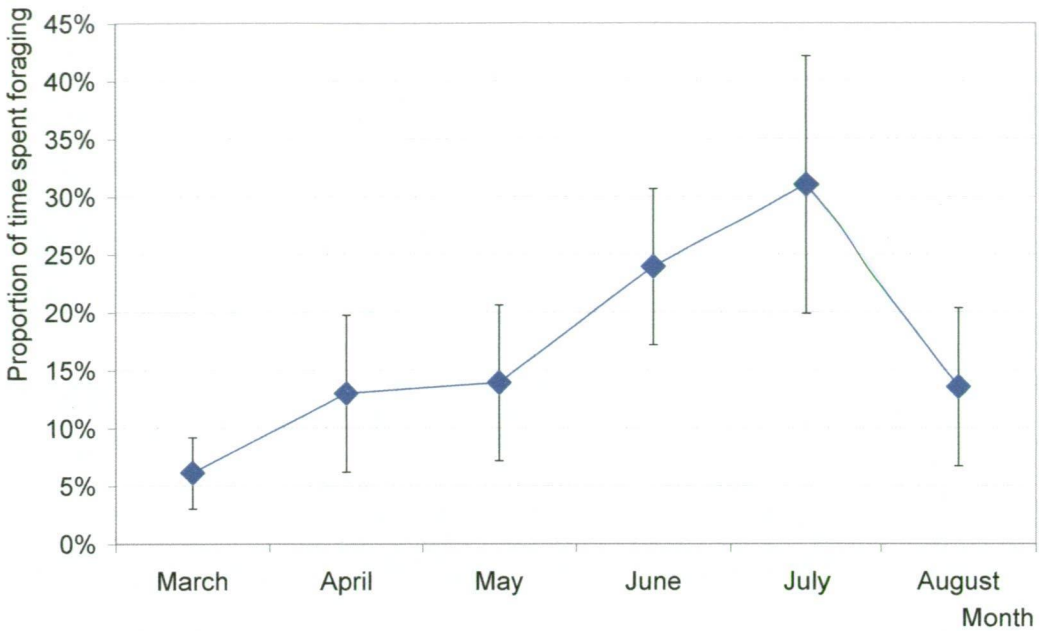


Figure 3.3 Mean (± SE) proportion of time Forest Ravens spent foraging by month. Proportion does not vary significantly across months ($F_{3,77}$ = 1.31; P = 0.269).

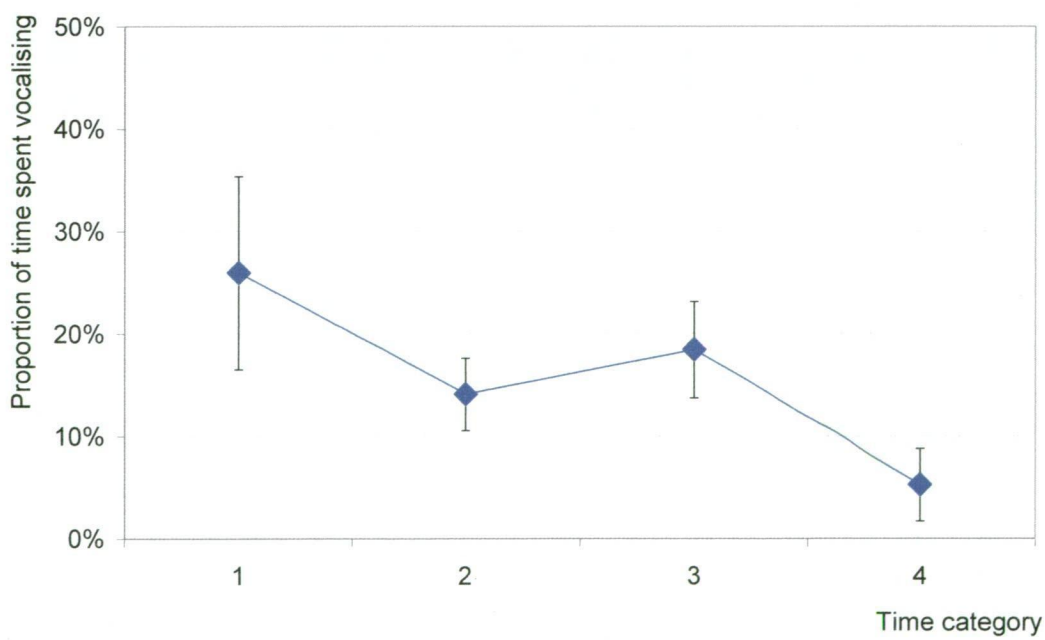


Figure 3.4 Mean (± SE) proportion of time Forest Ravens spent vocalising by time of day. Proportion does not vary across time categories ($F_{5,75}$ = 1.51; P = 0.220).

Outside the breeding season interactive behaviour, including courtship (1.49%) and aggression (1.70%) were rarely seen. Of four observations of aggression recorded in Autumn and Winter, two were directed at Grey Goshawks (*Accipiter novaehollandae*), one at a Swamp Harrier (*Circus approximens*) and one was directed at invading flock ravens. Three of the four records of aggression were made in July and August.

3.2.2 Breeding season activity-time budget

In Spring and Summer, 465 observations, forming 38 observation bouts, were made of Forest Raven behaviour. The behaviour observations undertaken in this study did not include observations of birds at or near the nest.

Figure 3.5 shows that surveillance was the most common activity undertaken by ravens away from the nest during the breeding season, accounting for 43.7% of observations. Foraging accounted for 21.3% of observations. The data were not analysed for monthly or diurnal variation due to the small numbers of observations and the inability to determine the gender and nesting stage of the focal raven, and therefore the proportion of daylight hours it was spending away from the nest. Similarly, no statistical comparisons could be made between the activity budget of ravens in the breeding (Spring and Summer) and non-breeding (Autumn and Winter) periods.

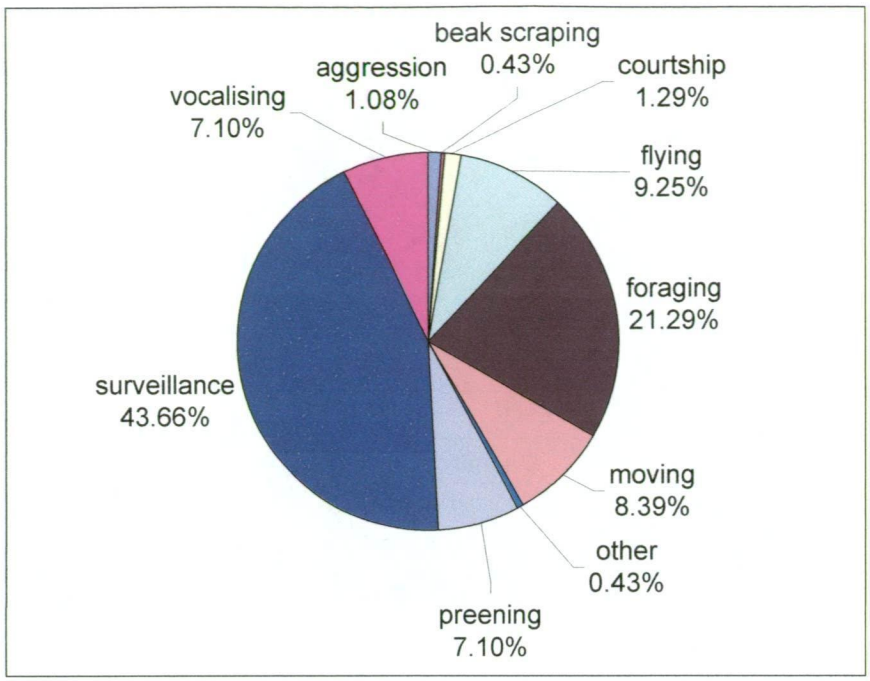


Figure 3.5 Proportion of time spent in various activities away from the nest by Forest Ravens in Spring and Summer

3.4 Discussion

3.4.1 Forest Raven activity-time budgets

This study investigated patterns of behaviour in adult Forest Ravens in Tasmania. The behavioural patterns of this species are consistent with that of other corvid species, in that surveillance and foraging were the most commonly observed activities.

In this study, only observations made in Autumn and Winter were analysed. While observations of Forest Raven behaviour were made in Spring and Summer, these only included ravens away from the nest. Earlier in this study (see Chapter 2) it was found that the amount of time ravens spend at the nest varies throughout the nesting season. Due to the inability to determine the stage of nesting each focal raven had reached, combined with the large variation in nest attentiveness among nesting attempts and the inability to determine raven gender, it was not possible to ascertain how much time a focal raven spent away from the nest, and thus an estimate of the total proportion of time spent in non-nesting activities could not be made. The Spring and Summer data collected in this study, then, are not directly comparable to those from Autumn and Winter.

Overall, perching behaviour, which includes surveillance, preening and territorial calling, accounted for the majority of observations in this study. Foraging was the second most commonly observed behaviour. Similarly, a study by Swinburne and Jessop on Little Ravens on Phillip Island, Victoria, found that "when Little Ravens were not roosting they were feeding" (Swinburne and Jessop 2005). A similar pattern of time-use has been found in Northern Ravens (Engel and Young 1992) as well as non-corvid species such as the Yellow-eyed Junco (Sullivan 1990) and the North Scandinavian Starling (Lundberg 1985). The negative relationship between surveillance and foraging behaviour, and their combined importance in the activity budget of the Forest Raven, can be seen in Figure 3.7.

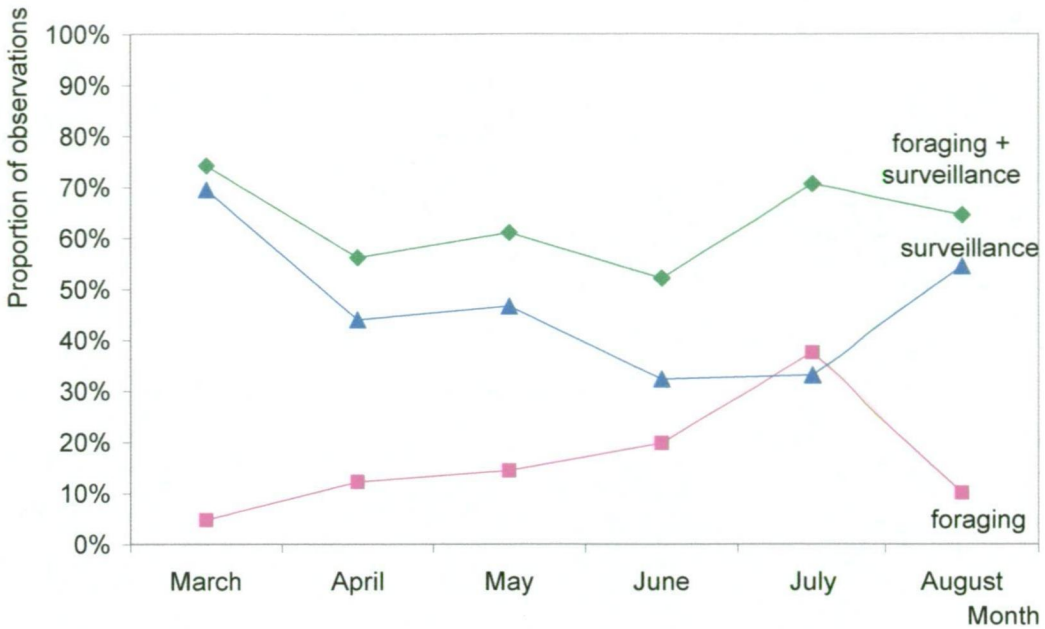


Figure 3.6 Proportion of time adult Forest Ravens spent in foraging and surveillance behaviours in Autumn and Winter

Foraging

Foraging is one of the most important activities of any animal, as it provides the energy required for other activities. In Forest Ravens, foraging was the second most commonly observed activity in Winter and Autumn, accounting for 16.9% of observations, and also in Spring and Summer, accounting for 21.3% of observations away from the nest.

Seasonal patterns of foraging behaviour have been recorded in a number of bird species (*e.g.* Moreno and Hillstroem 1992; Chapman and Paton 2005), sometimes varying between males and females. In Wheatears, for example, prior to nesting females increased foraging rates in order to put on energy reserves for egg production, while male foraging rates declined as they spent more time protecting their mates (Moreno and Hillstroem 1992). The efficiency of foraging at any given time may vary, however, depending on external factors such as prevailing weather conditions and seasonal or diurnal variation in specific food source availability (Verner 1965; Engel and Young 1992). It was expected that in Forest

Ravens foraging behaviour would increase towards the breeding season. As with female Wheatears (Moreno and Hillstroem 1992) female ravens would need to put on energy reserved for egg production and incubation. As Forest Raven nestlings, incubating and brooding adults, and juveniles were fed from caches near the nest, an increase in foraging rate may also be expected if these food caches were stocked prior to the onset of nesting. Towards the winter onset of nesting in Forest Ravens it is also possible that foraging efficiency may decline as production of insects decreases with decreasing temperatures (Verner 1965).

In the current study Forest Ravens exhibited no significant seasonal pattern in foraging rate outside the nesting season, although the data appeared to support the expectation that foraging rate would increase towards the breeding season. More data would be required to confirm this trend. Considerable variation existed in the frequency of observations of foraging within seasons. As foraging rate did not vary significantly with time of day, other unrecorded external factors are likely to influence foraging rate in Forest Ravens.

Surveillance

When perched, Forest Ravens were almost invariably alert, generally looking around but quick to look towards any disturbance nearby. As a result, for the purposes of this study ravens perched and not undertaking any other activity were considered to be in "surveillance" behaviour, but at times may instead have been resting; it was not possible to distinguish these two activities. Close human activity which was not directly focussed on a perched raven did not necessarily disturb the bird, but was apparently watched closely. On the other hand, any activity which was directed at a raven (for example, focussing binoculars on a perched bird), however discreet and distant, may scare the raven away. Heinrich (1989) suggests that Northern Ravens (*C. corax*) are "extremely sensitive to anything round and shiny, such as an eye or a camera lens". This, then, may also apply to binoculars or even obvious naked-eye observation of focal ravens.

In Autumn and Winter, surveillance accounted for 44.9% of observations, and 43.7% of observations away from the nest in Spring and Summer. The considerable amount of time in which Forest Ravens in this study were seen in surveillance behaviour may be in part attributed to their resident status, which generally leads to only one or two ravens perching together: the amount of time spent in surveillance behaviour by individual Carrion Crows decreased with flock size (Saino 1994). It is unclear why surveillance behaviour is so prominent in ravens. The typical perch high in a tree would virtually eliminate the risk of predation by mammals except, perhaps, humans. A fear of humans may be innate, having arisen from a long history of persecution (Heinrich 1999), however it is unlikely that many of the focal ravens in this study would have been directly affected by humans. A more likely explanation for almost constant alertness in Forest Ravens is the risk of predation from other birds, or the potential for conspecific intrusion into the territory.

Aggression

Physical aggression was rarely observed between Forest Ravens, but was more often seen between resident and flock birds than resident pairs and single or double intruders. Physical aggression generally comprised chasing behaviour, or swooping if the opponent was perched, accompanied by high-intensity calling, but twice in this study a mid-air conflict was observed, in which two ravens joined their feet and tumbled to the ground. Such behaviour, although rare, has also been reported in Australian Ravens (Rowley 1973b) and Common Ravens (Ratcliffe 1997). Ravens passing through the territory flew at high altitudes emitting a distinctive call ("transit contact call"; Rowley 1973b) and were generally ignored by the resident pair.

More commonly, aggression was shown towards other species, particularly raptors. Outside the nesting season, most raptors were ignored; however, Grey Goshawks (*Accipiter novaehollandiae*) and Wedge-tailed Eagles (*Aquila audax*) were the subject of strong aggression from Forest Ravens, the latter often being

mobbed by several pairs and the former generally chased by one or two neighbouring raven pairs. Ravens rarely appeared to have much impact on either of these species; numerous times a pair of ravens have been seen swooping on a perched Goshawk to no effect, despite their bigger size. Overall, aggression accounted for only 1.7% of observations outside the nesting season with the majority of aggression observations occurring in August. In Spring and Summer, the nesting season for Forest Ravens, aggression accounted for 1.1% of observations, all of which occurred in September. Autumn marks the onset of nesting for most Forest Raven pairs; the risk of nest predation by raptors, or potentially by intruding raven flocks (Yom-Tov 1974) may explain the increase in aggression seen at this time, when eggs are present in most nests.

Unnecessary beak wiping is known in corvids as a displacement behaviour, seen at times of mild tension or excitement (Goodwin 1977). In this study beak wiping, not associated with feeding or preening, was observed rarely and when seen occurred only briefly; consequently this activity accounted for fewer than 1% of observations in or outside the nesting season.

Outside the breeding season two "extra" adult ravens were sometimes seen in a territory, apparently tolerated by the resident pair. Because they could not be caught and banded, however, it was not possible to identify the ravens, resident or otherwise. This apparent tolerance of intruders during the non-nesting period, in conjunction with the increase in territoriality before the breeding season, suggest that territory boundaries may be relaxed during the year, then re-asserted prior to nesting. This is, however, speculative as exact territory edges were not known. Future studies into Forest Raven territory size and territorial behaviour would be of interest.

Vocalisation

Vocalising accounted for 14.6% of observations in Autumn and Winter and occurred primarily when a raven was perched; most vocalisation recorded was

territorial calling, but aggressive calling was also heard. Rowley (1973b) described a mild territorial call given by Australian Ravens, which may develop into a stronger territorial call; while these calls may occur at any time of day they are regularly given at dawn, presumably to advertise that the territory is still occupied (Rowley 1973b). There was no significant diurnal variation in vocalisation behaviour in Forest Ravens in the current study, although the data suggest that with greater sample sizes to reduce within-category variation a trend towards increased vocalisation early in the day may have been apparent. Such a trend would have been consistent with Rowley's description of territorial calling in Australian Ravens, although in the current study non-territorial vocalisations were included in the data.

Preening

Preening behaviour was closely associated with surveillance: a perched and alert raven was often seen to undertake brief bouts of preening, while 23 of 24 ravens seen preening exhibited surveillance behaviour in the sample point immediately before the preening bout began, or immediately after the preening bout ended. Self-preening was seen relatively infrequently, accounting for only 5% of observations outside the nesting season but slightly more, 7.1%, in Spring and Summer. Incubating or brooding ravens frequently preened upon leaving the nest (pers. obs.), due perhaps to the presence of insects in the nest as well as the feather-ruffling effect of sitting in a nest. While observations made at or next to the nest were not included in the current study, this may account for the apparent increase in preening also seen away from the nest in the nesting season. In Autumn and Winter, preening was the fifth most commonly observed activity and the proportion of time spent preening did not vary throughout the day. Conversely, preening or scratching accounts for much of the time Australian Ravens do not spend foraging, particularly in the middle of the day (Rowley 1973b).

Bonding activities

Allopreening was the main type of bonding activity observed in Forest Ravens. Overall, 1.4% of observations were of a pair of ravens in some form of courtship or bonding behaviour. Such activities, which also included huddling together, were generally accompanied by soft crooning noises by one or both of the pair. Rowley (1973b) refers to the "low murmur call" of Australian Ravens, which is made by members of a pair when they are perched together during an inactive period, particularly when allopreening. A similar call is also described by Secomb (2005b) for Northern Forest Ravens. Ratcliffe (1997) states that a range of 'cooing', 'crooning' and 'whining' calls have been recorded between Common Ravens. In most cases of allopreening the receiving bird was a willing participant, tilting its head to allow the other to gently probe or pull at the head and neck feathers. In other cases, the recipient moved away from the other; this sometimes resembled coyness, as the recipient moved short distances a number of times, with the offerer following each time. Eventually the recipient remained still and allopreening occurred. In some cases a bout of allopreening was begun by one bird soliciting from the other by sidling up and tilting its head to expose its neck feathers. 'Billing' (Wickler 1972) or 'allobilling' (Marzluff and Angell 2005), in which members of a pair lock beaks, was also observed in Forest Ravens, often associated with allopreening. As with many behaviours observed in this study, allopreening in Forest Ravens followed a very similar pattern to that seen in other corvid species (Marzluff and Angell 2005).

Pair interactions, including allopreening, were expected to increase before the onset of nesting, but in the current study too few observations of bonding behaviour were made to identify monthly or seasonal patterns. Allopreening is thought to be part of courtship in Northern Forest Ravens (Secomb 2005b), as it is in Little Crows (Debus 1996). While trust is required between allopreening birds, as the head and neck are vulnerable areas (Marzluff and Angell 2005), allopreening is also a functional activity, as a raven is generally unable to clean the feathers around its own head and neck of parasites (Rowley 1973b; Marzluff and Angell 2005), and thus is seen year-round. Australian Raven pairs were seen

to allopreen frequently in Autumn, although recrudescence of the gonads had not occurred at that time (Rowley, Braithwaite *et al.* 1973). In the current study, no instances of bonding behaviours were seen in summer; while this may be related to the small number of observations of this behaviour at any time, a similar pattern was also recorded in Australian Ravens, in which the bond between members of a pair is apparently weakest during the post-breeding moult (Rowley 1973b).

Flying

Overall, flying accounted for 12.2% of observations in Autumn and Winter, and 9.3% in Spring and Summer. It is likely that the time Forest Ravens spend flying was underestimated in this study: ravens fly fast, and long distances and are therefore soon out of sight from a stationary observer. Most observations of flying involved the flight of a raven which had been perched or foraging, away from the observation area; in such cases no more than three observations of flying were made before the focal raven was out of sight. This type of bias against behaviours which are seen only briefly, but may continue for some time away from observation, is a limitation of a study such as this. In the current study bouts with fewer than three observations were not recorded; if this study were to be repeated in the future, shorter observation bouts should be included to reduce this bias against flying.

3.4.2 Limitations of this study

Instantaneous sampling is a convenient and easy method of measuring behaviour, and can give a good approximation of the proportion of time spent in individual activities while allowing for a relatively large number of behaviour categories to be recognised (Martin and Bateson 1993). This technique, however, has inherent limitations. The exact duration of an activity bout cannot be recorded; furthermore, activities of duration shorter than the sampling interval may go

unrecorded if they fall between two observations. An appropriate sampling interval is short enough to reduce the chance of missing behaviour changes, while being long enough to ensure recorder accuracy (Martin and Bateson 1993). With this in mind, 30 second intervals were used in this study.

A study of behaviour such as this is subject to some bias, in that ravens are more conspicuous, and are more likely to remain in sight for the minimum time (3 observations) in some activities and some locations. It is likely, for example, that the proportion of time Forest Ravens spend flying has been underestimated in this study as ravens fly fast and are soon out of the visual range of the observer. Similarly, ravens foraging or moving on the ground were more likely to be disturbed, and consequently move out of the immediate observation area, than those in trees. Unfortunately, biases such as these are largely unavoidable and must be taken into account with the results of this study.

Despite apparent monthly and diurnal patterns in behaviour which correspond with recorded patterns for other corvid species, statistical analysis found no significant variation. In analysis individual observation bouts were used as samples. Forest Ravens tend to spend considerable time in some activities: ravens were seen in surveillance behaviour for up to 28 consecutive observations, and foraging for up to 23 consecutive observations. Most individual observation bouts in this study consequently comprised one primary activity, perhaps interspersed with occasional observations of other activities. As a result, for any given activity the proportion of time in which it was observed may vary from 0% to nearly 100% in different observation bouts. This produces very considerable variation among individual samples which may obscure statistical differences among seasons or time categories. Much longer observation bouts may reduce this problem, by increasing the likelihood of each individual sample providing an accurate overview of raven behaviour. This, however, would require considerably longer sampling intervals to reduce observer fatigue. In addition, due to the highly mobile nature of ravens longer observation bouts would also require ways of identifying and following the focal raven when it moved from the immediate

observation area. Although this has been undertaken for studies of other corvid species, such as the Northern Raven (Engel and Young 1992) it was not possible in the current study.

Many studies of bird behaviour and activity budgets have identified gender differences in time-use, particularly during the breeding season (Lundberg 1985; Moreno and Hillstroem 1992). This could not be tested in the current study due to the inability to determine gender of Forest Ravens.

3.5 Conclusion

This study investigated non-breeding behaviour of territorial adult Forest Ravens in Tasmania. Overall, the results of this study indicate that the behaviour of these birds is very similar to that of other corvid species, in that surveillance and foraging are the activities which account for most of the daylight hours. While some seasonal and temporal patterns in behaviour were apparent, these were not significant. This suggests that behaviour of Forest Ravens is relatively consistent throughout the year and throughout the day, but as raven behaviour varied considerably within diurnal and month categories true differences among categories may have been obscured. This may indicate a need for different methodology in a study such as this.

4. GENERAL DISCUSSION

4.1 Summary

This study investigated a number of aspects of the breeding biology and behaviour of the Forest Raven, *Corvus tasmanicus*, in Tasmania. Until now, much of the knowledge about the biology of the Forest Raven was assumed, from studies of the closely related Australian Raven and Northern Forest Raven. The results of this study indicate that the biology and behaviour of the Forest Raven is very similar to that of the other species of raven not only in Australia, but also to that of ravens from around the world. This study reinforces some previous records of Forest Raven biology, but also provides some novel information on the species.

The Forest Raven is a resident species, with breeding pairs holding extensive year-round territories and non-breeding birds forming nomadic floater groups. Forest Ravens are found throughout Tasmania, nesting primarily high in tall Eucalypt trees which provide a clear view in most or all directions. On average, nests measured in this study were located 24m above the ground, but heights varied between habitats, due primarily to the differences in available nest sites. Records from other sources indicate that ravens are flexible in their choice of nest sites, nesting on cliffs or in shorter trees where necessary. In a few cases observed in this study extra nests were constructed at the beginning of the breeding season; the purpose of these nests is not known, but they may be used as decoys, food cache sites or dormitory nests for recently fledged juveniles.

Nesting occurred in late winter and spring, the timing being similar to, but slightly later than, that of Australian Ravens and Northern Forest Ravens. In this, the results of the current study support the limited data already available (Higgins *et al.*, 2006), but reduce the differences in breeding season between the species. The incubation period of Forest Raven eggs, estimated from parental behaviour, was approximately 22-23 days after the onset of incubation: longer than the 20 days

assumed for the Northern Forest Raven (Secomb 2005b) and the 19-21 days of the Australian Raven (Rowley 1973c). Fledging periods in the Forest Raven ranged widely, from 37-43 days, but were consistent with those of other, similar-sized ravens (Madge and Burn 1994). Forest Raven brood-mates fledged from zero to six days apart.

The productivity of Forest Raven pairs in this study were comparable with other corvid species, with each pair producing on average 1.9 fledglings per season; productivity of individual pair-seasons ranged from zero to three fledglings, with most pairs producing two fledglings. This is comparable to the productivity of Australian Ravens and Northern Forest Ravens (Rowley 1973c; Secomb 2005b). Second clutches were laid in the event of the failure of the first clutch. While some pairs appeared to be consistently good breeders, and others consistently poor, the data were insufficient to test this statistically.

As with most corvids, both parents were involved in nest construction and care of the young. Although individual birds could not be identified, both males and females brooded nestlings to some extent, as evidenced by observed cross-overs in which one brooding bird was replaced by the other on the nest. Parental care of young included incubation of eggs, brooding of young nestlings and feeding of nestlings and juveniles. The amount of time in which the nest was attended by an adult, either sitting on the nest or feeding young, decreased throughout the nesting period. Similarly, the frequency of feeding visits to the nest decreased as nestlings aged, contrary to the pattern seen in Australian Ravens (Rowley 1973c). Away from the nest, during the breeding season territorial Forest Ravens spent most of their time in resting or surveillance behaviour; foraging was the second-most common activity of ravens at this time. A similar trend was seen outside the breeding season, in Autumn and Winter. The prevalence of perching and foraging behaviours in activity budgets is widespread in corvid and non-corvid species alike.

The behaviour of the Forest Raven during nest construction and the incubation and juvenile stages, as well as outside the nesting season, is similar to that of the Australian Raven. The overall nesting productivity of the two species is also similar. Forest Ravens do, however, appear to breed later and have longer nesting stages than Australian Ravens, and to be more successful in the production of second clutches. Overall, while the data were insufficient for statistical comparisons, the long-held assumption that the ecology of the Forest Raven matches that of the Australian Raven is supported by the results of this study, with some exceptions which should be considered in future studies.

4.2 Management of the Forest Raven

A knowledge of the behaviour and breeding biology of a species is a vital tool in management (Soh *et al.* 2002). A study into the relative importance of frequency and amount of food provided to nestlings of various corvid species was undertaken to increase growth and survival of captive-reared, endangered Mariana Crows and Hawaiian Crows (Whitmore and Marzluff 1998). Conversely, a study of preferred nest substrates was used to propose methods to reduce numbers of the House Crow, a pest species, in Singapore (Soh *et al.* 2002). It is hoped that the current study of Forest Ravens, by providing a basic knowledge of the breeding and behaviour of the species, may be of use in management of the species in Tasmania, as well as providing a basis for future studies.

Around the world, corvid species are becoming more urban. This is leading to problems as roosts are noisy and unsanitary, and breeding corvids may be aggressive to humans (Soh *et al.* 2002; Vuorisalo *et al.* 2003; Sinden and Jones 2004). The ready availability of food from anthropogenic sources such as waste disposal areas has created favourable conditions for increasing numbers and density of corvids in such areas (Marzluff *et al.* 2001), while food availability and lower predation risk has also increased the reproductive success of some suburban corvid populations (McGowan 2001). While no counts of Forest Ravens have

been made in Tasmania's cities, reports have been made of flocks in Hobart, and ravens in the same area have caused damage to buildings (Knowler 2004a; Knowler 2004b; Knowler 2004c). It appears, however, that large numbers of ravens are not yet invading urban or suburban areas permanently. Ravens in the current study were observed feeding themselves, or their young, with human food scraps. Although the diet of Forest Ravens has been described in some detail in the past (Higgins *et al.* 2006), new studies to determine the importance of human foods to Forest Ravens and the effects of increased availability of such foods on raven numbers would be of interest.

Forest Ravens, while apparently not yet causing problems in urban areas of Tasmania, are among other Australian corvids in causing problems in agricultural areas. In lambing paddocks ravens have been blamed for lamb and ewe deaths, although in most cases the birds are in fact scavengers rather than predators (Rowley 1969). Ravens are also problematic in orchards, damaging fruit and young shoots (pers. obs.), while commercial grains such as wheat and oats have been found in Forest Raven stomachs (Higgins *et al.* 2006). In Tasmania, the Forest Raven is not protected by law (Jones and Park 2005), and shooting and poisoning are accepted management techniques. The development of non-lethal management tools based on a knowledge of raven behaviour and ecology is desirable in these circumstances.

4.3 Limitations of the study and suggestions for further research

This study focussed broadly in the breeding biology and behaviour of the Forest Raven, and was limited by a number of factors, two of which relate to the biology of the study species: the location of nests and the innate intelligence and caution of the species. The other main limitation of this study was the inability to collect many breeding data for Forest Ravens and the dearth of existing information about the species.

Most Forest Raven nests in Tasmania are located high in the top or outer branches of tall trees, between 18 and 40m above the ground. As a result, the nests can only be accessed by an experienced and well-equipped climber. Frequent employment of such a person was not possible for this study, for financial, time and safety reasons. Attempts were made to install cameras at raven nests, thus allowing the contents of the nest to be viewed from the ground at regular intervals. This was found to be highly problematic, as the cameras could be installed only at nests which could be safely accessed by an experienced climber, and which had appropriate branches nearby to which the camera could be attached. Cameras were eventually installed at three nests: one camera captured some images of nestlings before failing; a replacement camera moved in strong winds and no longer gave a view of the nest contents. In the other two cases the ravens abandoned the nest soon or immediately after installation of the camera. The use of cameras was therefore abandoned and clutch size, egg survival and hatchability and nestling survival could not be ascertained in this study. As collection of these data were initially primary aims of this study, the focus of the study had to be changed after the second nesting season; in some aspects of this study fewer than optimal results were collected due to the relatively short amount of time available for data collection in these areas.

Identification of individual Forest Ravens was also not possible, as birds could not be captured and banded. Adult ravens are innately cautious of unfamiliar objects

and appear to be particularly wary of traps; this has also been reported in other corvid species such as the Northern Raven (Heinrich 1989; Ratcliffe 1997; Heinrich 1999; Marzluff and Angell 2005). Juveniles were less cautious, but were apparently warned away from the trap by their parents; adult ravens vocalised loudly when juveniles approached the trap. A number of trap and bait types were used, including a trap design which has been used successfully on flocks of Australian Ravens (Rowley 1968). Traps were left in place (closed) for some time before they were baited, but all trapping attempts were unsuccessful. As a result, a number of assumptions about the identity of individual ravens, such as incubating birds and juveniles, were necessary in this study. The lack of sexual dimorphism in Forest Ravens also prevented the development of gender-specific activity-time budgets; differences in the activity budgets of males and females have been reported in many bird species.

The results of this study have been compared with those of Rowley's study of Australian Ravens (Rowley 1973c; Rowley, Braithwaite *et al.* 1973). The current study was necessarily undertaken over a shorter period than that of Rowley's, and therefore contains many fewer data for comparison. The geographical scale of the current study was also small, with focal territories located only in a single habitat type. Furthermore, in the current study only observational data could be collected, as opposed to the more comprehensive data from shot individuals (Rowley, Braithwaite *et al.* 1973). Very few existing data for Forest Ravens were available to add to those collected here. Consequently, it must be noted that the results of this study may not be truly accurate for the Forest Ravens as a species. True measurements of mean nesting success and productivity can only obtained through very large sample sizes, collected from a range of habitat types.

Within its limitations, the broad nature of this study was intended to provide a basis for future, more specific studies of the Forest Raven. As such, it raises a number of questions and the need for clarification of some apparent trends: the consistently successful breeding of some pairs over others; the purpose of the extra nests sometimes built at the beginning of the season; patterns of time-use

over diurnal or seasonal gradients. An activity-time budget study for a species, such as developed here, is often the precursor to the development of an energy budget; this could be undertaken in future studies. Finally, studies into the behaviour of young ravens after they leave the natal territory, and of flocks, are necessary for effective management of the Forest Raven but were outside the scope of the current project.

As the only corvid species in Tasmania, the Forest Raven is an important part of Tasmania's avifauna. From an ecological, social and economic standpoint, the Forest Raven is deserving of continued study and greater knowledge by science and society alike.

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